ABSTRACT

Title of Thesis:	SEASONAL MIGRATIONS OF ATLANTIC STURGEON AND STRIPED BASS THROUGH THE MARYLAND WIND ENERGY AREA
	Ella Rothermel, Master of Science 2019
Thesis Directed By:	Professor Dr. David Secor, Marine, Estuarine, and Environmental Science

Baseline information is needed on migrations through US Mid-Atlantic Bight shelf waters in advance of offshore wind development. Acoustically-tagged Atlantic sturgeon and striped bass were detected from 2016-2019 in an array of 20 acoustic telemetry receivers centered on the Maryland Wind Energy Area and extending 10-50 km offshore. Both species were transient (mean residency < 3 days), but migration patterns differed seasonally and were related to depth and temperature. Generalized additive models showed that Atlantic sturgeon occur at inshore sites during spring while striped bass shifted toward the outer shelf as inshore waters cooled in winter. The movement of hundreds of tagged striped bass and sturgeon, originating from shelf waters from Maine to South Carolina suggests that the Wind Energy Area is part of a multi-species Atlantic coastal flyway, particularly during spring, fall, and winter periods. Thus, summer presents a potential window for wind tower construction.

SEASONAL MIGRATIONS OF ATLANTIC STURGEON AND STRIPED BASS THROUGH THE MARYLAND WIND ENERGY AREA

by

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South Carolina Rivers; DE Coast = Atlantic Coast of Delaware; VA = Virginia Rivers. Striped bass tagging regions are: Hudson = Hudson River, New York; Potomac = Potomac River, Maryland; MA = Coastal Massachusetts; Kennebec = Kennebec River, Maine.

Appendix

Table A.1. Characteristics of the 40 striped bass tagged between 4/21/17 and 5/11/17 in the Lower Potomac River, Point Lookout State Park, MD and off the coast of Massachusetts. All fish were surgically implanted with depth-transponding acoustic transmitters (VEMCO®; model V16P-4H-S256; 67 mm, 10 g, 2.5 year expected battery life).

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Chapter 1: Introduction

Background

Importance of migration flyways

The ecological and societal services provided by marine fishes are structured by the timing and extent of their migratory behaviors (Deegan 1993; Sheaves 2009; Secor 2015). Across animal taxa, migrations are characterized by directed and persistent movements between distinct habitats that allow species to periodically exploit environments that offer favorable physiological conditions, increased foraging opportunities, or greater reproductive success (Alerstam 1993; Metcalfe et al. 2002; Dingle and Drake 2007). Migrations are thus essential to the persistence of marine fish species and act as a mechanism that functionally extends and distributes populations, along with their associated services, between disparate locations. Although migrations are often understood through the context of endpoints or stopovers (e.g. spawning grounds, feeding aggregations), the pathways between these areas are equally important.

The importance of migration pathways has long been appreciated in bird ecology, where the term “flyway”, originally conceived to aid in the management and conservation of migratory waterfowl populations, is used to define routes and networks of migration pathways that connect habitats (US Department of the Interior 1959; Lincoln 1979; Hawkins et al. 1984). Flyways function as transit routes between migratory destinations, but contain regions where individuals may dwell for extended periods of

time to rest or feed (Boere and Stroud 2006). Though species and individuals are expected to vary in their specific use of a migration corridor, the multi-species flyway concept emphasizes the broader ecological significance of geospatial routes that may extend over multiple jurisdictional boundaries. Migratory bird research and conservation has thus benefitted from the recognition that cooperative efforts across jurisdictions to preserve flyways confers connectivity and success to a diversity of species. The field of fish migration ecology has yet to adopt this perspective, due in part to the comparative difficulty of capturing, tagging, and observing animals in aquatic environments (Metcalfe et al. 2002; Secor 2015). Only recently have researchers begun to describe the broad-scale movement patterns of marine species; however, findings increasingly suggest that marine taxa utilize similar predictable movement corridors that function much like avian flyways (Block et al. 2011; Secor 2015; Horton et al. 2017).

Despite supporting diverse and abundant fisheries, the potential for shelf waters of the US Middle-Atlantic Bight (MAB) to operate as a multi-species flyway has received little attention. The MAB is connected to multiple crucial estuarine nursery and spawning habitats and is among the most productive coastal systems globally (O'Reilly and Busch 1984). However, the US East coast also experiences large changes in seasonal temperature (Δ 18°C sea surface temperature; He et al. 2010; Richaud et al. 2016), which shape regional shelf ecosystems. Regional fish migrations are accordingly structured by isotherms (Grosslein and Azarovitz 1982; Collette and Klein-MacPhee 2002; Able and Brown 2005), with many species traveling in a North-South direction along the MAB to maintain progressively favorable conditions. Though endangered and economically-important taxa alike are seasonally concentrated within this multi-species flyway,

patterns of shelf distribution and habitat selection are incompletely understood. The remote nature of the coastal environment has precluded in-depth investigations of such behavioral information in the past, but emerging bio-logging technologies present a valuable opportunity to evaluate the incidence of critical species within the MAB migration corridor (Lowerre-Barbieri et al. 2019).

Emerging concerns and opportunities for research

Globally, marine fisheries are threatened by fishing pressure and climate change, both of which will alter species distributions and viability (Field et al. 2001; Perry et al. 2005; Daskalov et al 2007; Nye et al. 2009; Pinsky et al. 2013). Migratory animals range widely, but their reliance on specific seasonal habitats may increase their vulnerability to anthropogenic impacts (Robinson et al. 2009). Of particular concern, multiple regions along the US. East Coast continental shelf have been leased for the future development of renewable wind energy sites, which are slated to occur in areas that directly overlap with the MAB migration corridor. Construction and maintenance of wind power facilities will have localized impacts, but the widespread extent of development may fundamentally alter the regional function of the shelf flyway among individuals and populations. In order for fisheries management to remain effective in this changing environment, increased knowledge of multi-species use of the MAB flyway, along with information on the current drivers and constraints to regional species migrations, is needed.

Recent technological advancements in bio-logging, and more specifically, the ease of acoustic telemetry methods, is rapidly expanding the ability to understand and describe the hidden behaviors of fish (Cooke et al. 2004; Hussey et al. 2015). Acoustic

telemetry, which uses high-frequency transponding tags to remotely record and track individuals, has facilitated new discoveries regarding fish movement patterns and habitat use that could not have been elucidated by mark-recapture methods of the past (Bolle et al. 2005; Secor 2015). Improvements in the battery life of tags and the acoustic-release capabilities of receivers have further increased the range of spatial and temporal scales in which acoustic telemetry studies can be employed. The prevalence of telemetry has also led to an expansion in the number of species tagged, which through data-sharing agreements, can increase sample sizes and strengthen population-level inferences. The current state of acoustic telemetry in the MAB thus provides a unique opportunity to examine fish migrations through coastal shelf waters.

In this thesis, I leverage the robust monitoring capabilities of new receiver technologies and the widespread availability of acoustically-tagged fish in the MAB to understand how this region functions as a multi-species flyway. Specifically, I will use acoustic telemetry to evaluate the migration patterns of two model species of management concern: endangered Atlantic sturgeon (*Acipenser oxyrhynchus*) and economically important striped bass (*Morone saxatilis*). Both species are anadromous (tidal freshwater spawning) with wide-ranging coastal migrations, but differ in their ecology and life history. Thus, Atlantic sturgeon and striped bass can exemplify the overlapping but variable uses of a migration corridor. By examining individuals from a range of populations, over relevant spatial and temporal shelf gradients, I provide comparisons of species behavior and habitat use that can be used to inform conservation and management strategies in the MAB. In Chapter 2, I compare the distribution and timing of Atlantic sturgeon and striped bass incidence on the MAB shelf and examine the

potential habitat associations of these patterns. I also compare the degree of residence and transit behavior between the focal species. In Chapter 3, I determine the spatiotemporal drivers of species abundance and individual residence. The second chapter is intended to compare how Atlantic sturgeon and striped bass currently use shelf habitat while the third chapter aims to formulate models that can aid management by predicting when species occur in the area and how they might be differentially affected by impending future changes.

Thesis Overviews

Funding support

Thesis funding support was provided by the US Department of the Interior, Bureau of Ocean Energy Management (BOEM), Office of Renewable Energy Programs, Sterling, VA, under Agreement Number M16AC00008 to D. Secor and H. Bailey. The objective of the award was to quantify the seasonal transit and habitat association patterns of migratory Atlantic sturgeon and striped bass through the proposed Maryland Wind Energy Area (MD WEA).

Chapter 2: Comparative migration ecology of Atlantic sturgeon and striped bass in the US Mid-Atlantic Bight flyway

Atlantic sturgeon and striped bass, two anadromous species of concern, are known for their extensive migrations along the US Middle-Atlantic Bight. Though patterns of habitat selection have been described for these species within spawning rivers

and estuaries, the timing and distribution of their presence in coastal shelf waters is incompletely known. Using a gradient-sampling array of acoustic telemetry receivers, I compared the seasonal incidence and movement behavior of target species in the near-shelf region of Maryland over a 25-month period. Atlantic sturgeon incidence was highest in the spring and fall and tended to be biased toward shallow regions (10-20 m) while striped bass had increased presence during the spring and winter months and were more likely to select deeper waters (20-40 m). Despite relative transience in the study area, both species spent more time in shelf habitat during autumn and winter, particularly striped bass, with many individuals exhibiting prolonged presence on the outer shelf during winter. Movement corridors also differed spatially between northern and southern migrations for both species, but appeared to be influenced by temperature; striped bass selected relatively cooler conditions while Atlantic sturgeon preferred warmer temperatures.

The manuscript for this chapter has been distributed to study co-authors and is currently being revised based on their edits. Before final submission, I will obtain necessary permissions from BOEM. The target journal for the manuscript is PLoS One and the resulting paper is intended to be open-access.

Chapter 3: Environmental and individual drivers of Atlantic sturgeon and striped bass occurrence in the Maryland Wind Energy Area

Wind energy development along the US East Coast is likely to impact critical migratory species that rely on the region as a transit route between seasonal habitats. Information on the environmental and individual drivers of occurrence is needed to

minimize harmful interactions with species of concern and to assess potential future behavioral changes caused by increased activity and structure in shelf waters. In order to obtain the breadth of environmental and population information necessary to inform predictions, data were obtained and modeled from a gridded acoustic telemetry array deployed for two years along a cross-shelf gradient (same as described in Chapter 2), which censused acoustically-tagged Atlantic sturgeon and striped bass belonging to different potential migration groups identified by where they were tagged. I used Generalized Additive Mixed Models (GAMMs) to determine the influence of seasonal and environmental factors on the daily relative abundance and weekly residence of both species. Depth, day-of-year, sea surface temperature change, and chlorophyll-a concentration were significant predictors of abundance for both species. However, functional responses differed: Atlantic sturgeon were predicted to be more broadly distributed over the shelf region in autumn compared to the spring, while probability of occurrence for striped bass was highest during the winter months and lowest during the summer. Further, striped bass shifted to deeper waters during winter as sea surface temperatures cooled and were influenced by temperature changes on longer time scales compared to Atlantic sturgeon. Individual residency largely aligned with broader abundance predictions in that Atlantic sturgeon were likely to spend more days in the area during spring and fall with a peak in residency near 18°C, while striped bass were more likely to reside in the area longer during winter and when temperatures were cooler, between 5-10°C. There were only subtle differences in residency response between tagging origins.

This Chapter has not been yet prepared for manuscript submission.

Implications and future studies

My thesis findings indicate that although Atlantic sturgeon and striped bass were mostly transient in Maryland's shelf waters (residency < 3 d), there were fundamental differences in the regional migration patterns along the southern MAB flyway. Seasonal distribution of both species overlapped with the proposed MD WEA, but Atlantic sturgeon were more biased toward shallow, near-shelf depths and striped bass were more likely to occur in deeper areas. Additionally, Atlantic sturgeon displayed broader temperature tolerance, while striped bass tended to be associated with a relatively cool and narrow range of temperature conditions. Migration behaviors also varied between migration seasons, with Atlantic sturgeon being more broadly distributed in the autumn compared to the fall and striped bass exhibiting rapid northern spring migrations but prolonged winter presence near outer-shelf regions. There was evidence of individual and group-level variability in shelf presence, but relative species abundance was effectively modeled using only a few environmental and seasonal predictors.

The sampling design of the gridded receiver deployment over relevant spatiotemporal scales allowed key inferences related to shelf and oceanographic gradients pertinent to future wind energy development. Summer months present a favorable window for wind tower construction, which would minimize interactions with striped bass and Atlantic sturgeon. The derived habitat and residency models also serve as a baseline with which to compare future incidence and behavior of these migratory species during wind farm installation and operation phases. Future research will be needed to fully assess impacts of changes in the MAB and these evaluations may benefit from the use of similar gradient-based designs; these will not only maximize the effectiveness of

monitoring, but will provide a broader context for the scale of impacts that may occur due to wind energy development.

My findings offer novel insight on the movement ecology of marine fish within migratory corridors and emphasize the importance of preserving such flyway habitats. In contrast to my original hypotheses, Atlantic sturgeon displayed rapid transit along the shelf and striped bass appeared to use deeper waters as winter habitat. These behaviors may be region-specific and do not preclude complex and variable movement patterns between individuals and populations. However, the unexpected nature of my results highlights the need to better appreciate the myriad ways marine taxa utilize the MAB flyway. Cooperation among researchers, expanded scale of acoustic telemetry arrays, and increased incorporation of oceanographic variables, physiological data, and individual characteristics will all serve to improve understanding of critical migration corridors.

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Chapter 2: Comparative migration ecology of Atlantic sturgeon and striped bass in the US Mid-Atlantic Bight flyway

Introduction

Although broad-scale migration patterns for many marine species are well documented, these are chiefly known by stopover points (e.g., natal spawning areas, coastal feeding habitats) rather than the flyways (transit regions) themselves. Seasonal migrations through flyways allow individuals and collective groups to change habitats that favor bioenergetic capacities, prey availability, and reproductive success (Nathan et al. 2008; Secor 2015; Walther et al. 2015). Endangered Atlantic sturgeon *Acipenser oxyrhynchus* and economically-important striped bass *Morone saxatilis* are coastal species that migrate along the shelf region of the MAB. Though both species rely on coastal migration corridors to connect seasonal habitats, the timing and distribution of their movements in near-shelf waters are incompletely known. Recent advances in biotelemetry (Cooke et al. 2004; Hussey et al. 2015) present a valuable opportunity to compare and contrast seasonal patterns of shelf movement between Atlantic sturgeon and striped bass, which are both known for their extensive coastal migrations but differ in their life history and movement and feeding ecology.

The comparative migration ecology of striped bass and Atlantic sturgeon likely relates to differing foraging and locomotion behaviors, reproductive cycles, and thermal preferences. Atlantic sturgeon are a large, long-lived, anadromous demersal benthivore that range widely in near-shelf waters of the northwest Atlantic (Florida to Quebec).

Generally, adult Atlantic sturgeon undertake migrations from the south Atlantic Bight and southern MAB as far north as southern New England in the spring and return south in the fall and winter. Atlantic sturgeon tend to remain in relatively shallow areas close to shore (10-50 m depth) in the MAB, with a broader shelf distribution in autumn compared to spring (Stein et al. 2004; Laney et al. 2007; Erickson et al. 2011). Like sturgeon, striped bass are anadromous (spawning in spring), however in contrast, they are highly-mobile pelagic and epi-demersal predators that exhibit complex and diverse movement patterns. While some individuals remain in estuaries their entire lives, other population contingents, particularly those originating in the Chesapeake Bay and Hudson River, migrate into coastal waters from the Bay of Fundy to Cape Hatteras, North Carolina (Clark 1968; Secor and Piccoli 1996; 2007). Generally, mid-Atlantic striped bass >80 cm total length (TL) become ocean migrants that move northward in the spring and southward in the fall (Waldman et al. 1990, Dorazio et al. 1994; Secor and Piccoli 2007). Coastal telemetry arrays have confirmed southerly movements of individuals in the fall and northerly movements in the spring, with some evidence for slightly faster northward migrations (Kneebone et al. 2014).

Here, I utilized an acoustic telemetry array designed to sample across key environmental gradients and leveraged the large number of acoustically-tagged Atlantic sturgeon and striped bass active within the Northwest Atlantic to describe seasonal incidence and distribution patterns within this MAB flyway. I further evaluated habitat associations and transit rates. Based on species ecology, I hypothesized that Atlantic sturgeon would transit more slowly through the shelf region, as they may forage within coastal migration corridors. Unlike Atlantic sturgeon, adult striped bass are pelagic

predators that rely on mobile prey as a food source and are often associated with structure (Haeseker et al. 1996; Tupper and Able 2000; Harding and Mann 2003). Due to the relatively featureless nature of the southern MAB, I anticipated that striped bass would move more rapidly through these shelf waters.

Study site

The MAB consists of a relatively broad (50-200 km wide) shelf area that stretches from Cape Hatteras, North Carolina to the southern flank of Georges Bank off Massachusetts. Biological dynamics in the MAB are tied to seasonal changes in stratification. During summer, the cessation of strong winds, combined with rapid increases in atmospheric temperature, creates a persistent thermocline that extends over much of the shelf (Houghton et al. 1982; Lentz 2017). Deeper winter waters maintain relatively constant temperatures even as surface waters warm, resulting in a "cold pool" bounded by warmer near-shelf waters and dense, saltier waters at the shelf break (Houghton et al. 1982, Rasmussen et al. 2005). Summer months below the thermocline are therefore characterized by a cross-shelf gradient of decreasing temperature with distance from shore. With the onset of fall, cooling of surface waters, along with wind-driven mixing and storm events that increase bottom water temperatures, destratify the Mid-Atlantic water column (Castelao et al. 2010; Gong et al. 2010; Lentz 2017). Shelf water temperatures are thus relatively homogenous throughout the water column during winter months, though a cross-shelf gradient still exists with more rapid shelf cooling in shallow waters and comparatively warm waters at the outer shelf. South of Hudson Canyon, the MAB is a relatively homogenous and flat seabed habitat, composed

primarily of soft sediments (Stumf and Biggs 1988; Poppe et al. 1994). The shelf habitat off Maryland exemplifies this pattern; sediments are mainly sandy with low relief and little topographic complexity (Figure 2.1). However, there are also gravel and mud patches, sand megaripples, areas of higher slope, and soft coral habitats that could influence the behavior of fish moving through the area (Guida et al. 2017).

Methods

Acoustic telemetry array

Movements of acoustically-tagged fish were recorded from November 2016 until December 2018 using a primary array of 20 fixed acoustic-release receivers (VR2AR, 69 kHz; Vemco, Bedford, Nova Scotia, Canada) deployed in a gradient design. Here, environmental variables were expected to grade continuously on a spatial and temporal basis; the array design was intended to fully encompass these cross-shelf gradients by placing receivers at locations to capture this gradient but also target movements through the MD WEA. A central and high-density receiver stratum (Middle) was located within the central shelf region. Inshore (Inner) and offshore (Outer) strata of less densely distributed receivers were adjoined to this central array (Figure 2.1). The high density of receivers in the central stratum was intended to provide higher-resolution data for baseline movement information within a federal wind farm lease area (MD WEA: Maryland Wind Energy Area). Receivers were thus positioned across broader shelf gradients 10-50 km from shore and 10-45 m depth (Figure 2.1). Based on the *a priori* expectations of a 1000 m maximum detection radius, receiver spacing allowed for

approximately 50% detection probability in the Middle and 20% detection probabilities in the Inner and Outer strata. The acoustic-release receivers were suspended in the water column 1 m from the seafloor using a 25-cm diameter hard float and two 20.5 kg iron weight plates. Receivers continually recorded detected transmitters, and logged tilt, ambient noise, and bottom temperature on an hourly basis. Data were downloaded approximately every 4 months during maintenance cruises. Supplemental detection data were gathered outside the primary Maryland array through collaborations with researchers in the Atlantic Cooperative Telemetry (ACT) Network (www.theactnetwork.com).

Striped bass tagging and available tags

During the period of receiver deployment, >500 striped bass and >1000 Atlantic sturgeon implanted with active transmitters were at large within the Mid-Atlantic Bight and southern New England (Secor 2019). An additional 40 large striped bass were implanted with transmitters to obtain depth-at-transit information for individuals which were highly likely to move through the array (Kneebone et al. 2014). A portion of these fish (n=28) were sampled from a pound net in the lower Potomac River, Point Lookout State Park, MD during April – May 2017 and 2018 (Appendix, Table A.1). Additional tagging of a subset of large striped bass occurred off the coast of Massachusetts during August - October 2017 (Appendix, Table A.1) Fish were surgically implanted with VEMCO®; model V16P-4H-S256 transmitters according to tested (Wingate and Secor 2007) and IACUC-approved surgical protocols, which included use of the anesthetic

Aqui-S 20E under a US Fish and Wildlife Service Investigational New Animal Drug permit.

Data analysis

Prior to analysis, all acoustic data were filtered to eliminate codes only heard once to help correct for false detection and code collision (Pincock 2012). Detection data for each transmitter (individual) was compiled to provide incidence at hourly and daily time steps. Temporal patterns in incidence were investigated using generalized autoregressive moving average (GARMA) models to accommodate the non-Gaussian (discrete and zero-inflated) distributions (Benjamin et al. 2003). Two Fourier series of sinusoidal functions, $\sin(2\pi t/d)$ and $\cos(2\pi t/d)$, where period d is one day or one year, and t is the hour-of-day or day-of-year, respectively, were added as explanatory variables to determine temporal patterns (Wingfield et al. 2017). Here, day-of-year assesses seasonality while hour-of-day describes diel cycles. Models were fit using the gamlss.util package in R (Stasinopoulos and Rigby 2017) and were selected by Akaike's Information Criterion (AIC) comparison. Autocorrelation and partial autocorrelation plots were examined for remaining serial dependence in the model residuals and residual plots were used to assess the overall model fit. Daily incidence (no. individual fish d^{-1}) was summed by receiver to evaluate broad-scale differences in number of individuals detected between seasons and region (Inner, Middle, Outer). For all analyses, seasons were divided equally and defined as winter (Dec, Jan, Feb), spring (Mar, Apr, May), summer (Jun, Jul, Aug), and autumn (Sep, Oct, Nov). Because daily incidence data were zero-inflated and skewed, non-parametric Kruskal-Wallis one-way analysis of variance and post hoc Dunn's test with

the Bonferroni method for multiple comparisons were used. Analyses were conducted using R 3.5.1 (R Development Core Team; www.r-project.org) and ArcGIS 10.1 (Environmental Systems Research Institute).

Spatial patterns of site (receiver) usage within the gradient array were assessed using the Optimized Hot Spot Analysis tool (Getis-Ord Gi*statistic) in ArcGIS. Separate analyses were conducted based on the number of unique individuals detected daily at each receiver within each season and over all seasons and years combined.

Single Parameter Quotient analysis (Lluch-Belda et al. 1991) was used to investigate the selection behavior of each species for bottom temperature in each season. Daily presence of fish was compared to all bottom temperatures when fish were either present or not within seasons. Temperature values were binned so that each interval contained a range of 2°C to reflect regional and seasonal variability. For each season and temperature interval, a Quotient index (QI) was calculated as

$$QI_i = \frac{\%Observed\ Detections}{Env.Var.Freq_i \times 100}$$

where i is i-th frequency histogram interval and Env.Var.Freq gives the distribution of daily temperature values recorded in each environmental variable interval for the season. A value of QI=1 represents even distribution across habitat types, QI>1 indicates preference, and QI<1 indicates avoidance. Significant deviation from QI=1.0 was tested through bootstrapping. Confidence intervals (CI) were calculated based on the null hypothesis of a random association between biological and environmental variables. QI values lying outside of the CI curve indicate significant selection or avoidance.

Indices of residency and transit were calculated from individual data aggregated into broad autumn/winter and spring/summer periods to facilitate comparisons between northern and southern migrations for each species. Residency was calculated using daily incidence data and the V-Track package in R (Campbell et al. 2012; c/o Franklin Ecolab, The University of Queensland, St Lucia, Qld, Australia). The RunResidenceExtraction function was used to determine when tagged striped bass and Atlantic sturgeon were within the detection field of a given receiver. Each detection event for a tagged fish was initiated when the individual first moved into the detection field and was recorded two times. Detection events were then terminated when the tag was detected at a different receiver or if no new detections were recorded for 12 hours. Residence events were summed for each fish and each migration season and reported as hours detected. Cumulative unique days detected for each individual per season were also calculated to provide a comparative, coarse measure of residence. Differences in residence periods between species and seasons were compared using Wilcoxon rank sum tests.

Speed of transit was estimated only for striped bass based on transit from the MD acoustic telemetry array to a nearby array in shelf waters off the Delaware Bay, an array centered in the Delaware Wind Energy lease area (Figure 2.1). Existing data sharing agreements did not support a complementary analysis for Atlantic Sturgeon. Transit events were defined as directed one-way movements. Each transit event was classified as north or south and rate of transit was calculated as the distance (km) between the two receivers divided by the amount of time (h) between detections. Differences in log-transformed swimming speed between direction (north vs. south) were evaluated using Student's t-tests. Transit rates were further tested for differences according to life history

characteristics using linear mixed effect models (LMMs) in the R package nlme (Pinheiro et al. 2017). Rate of transit was the dependent variable with year, season, and sex as categorical variables and body size at tagging (TL in cm) as a continuous covariate. LMMs for log-transformed transit rate only included fish tagged in the Potomac and Hudson Rivers; tagging region was not investigated as a fixed effect due to limited sample size. Unique individual (tag code) was added as a random effect in the models to account for repeated measures. The full model contained all biologically-relevant two-way interactions, including Sex*Season, TL*Season, and TL*Sex.

Results

Detections

Following removal of single detections, a total of 352 individual Atlantic sturgeon and 315 individual striped bass were detected by the coastal MD array between November 2016 and December 2018. Most detected Atlantic sturgeon were originally tagged off the coast of Delaware or in the James River (Table 2.1). Detected striped bass were tagged in the Potomac, Hudson, and Delaware Rivers as well as summer feeding grounds in coastal Massachusetts (Table 2.1). Nearly half of the Atlantic sturgeon were detected during a single migration season alone (174 fish, 49%); 34% and 14% were detected in two and three separate seasons, respectively. Of the remaining 9 fish that occurred in >3 seasons, most were tagged off the coast of Delaware (n = 6). Acoustically-tagged striped bass had an overall higher seasonal fidelity to the array, with 41%, 34%, and 25% of individuals detected across ≥ 3, 2, and 1 seasons.

Temporal patterns of distribution

Seasonal components (sine and cosine transformations of day-of-year) were retained as highly significant in the final GARMA models for both species (Table 2.2). Atlantic sturgeon occurred over broad periods during early spring to early summer and early autumn to early winter each year (Figure 2.2), with very few detections during late-summer or winter months. Compared to Atlantic sturgeon, striped bass had a higher mean number of individuals detected on each receiver per day (Figure 2.2). Additionally, striped bass exhibited more sporadic but concentrated seasonal incidence; greater numbers of individuals occurred December-February and early April both years. Striped bass were consistently absent from the array across summer and autumn months. Hour of day was only retained as a significant predictor in the final GARMA model for striped bass incidence (Table 2.2). Striped bass were more likely to be detected within the array during daylight hours, especially during winter months (Figure 2.3). Atlantic sturgeon lacked a diel pattern among seasons. Although cyclic patterns were identified in GARMA model residuals for both species, these likely reflected the exceptionally zero-inflated distribution of individual hourly detections. Residuals were, however, normally-distributed and lacked temporal autocorrelation, indicating that models adequately fit the daily and seasonal detection patterns.

There were significant differences in the number of individuals detected seasonally for each species (Table 2.3). Pairwise comparisons using Dunn's post hoc test showed that more Atlantic sturgeon were detected during autumn compared to all other seasons and that individual incidence was greater during the winter than the summer.

Incidence did not differ between spring and summer or winter and spring. Striped bass pairwise comparisons showed significant differences in incidence between all seasons except between spring and winter. Individual incidence was highest in the winter and lowest in the summer.

Cross-shelf strata differences were evident across all seasons (Table 2.3). Pairwise comparisons of numbers of individual Atlantic sturgeon were significant for all strata with the Inner stratum exhibiting nearly 3-fold higher average incidence than the Middle and Outer regions, and the Middle stratum having higher individual incidence than the Outer stratum. In contrast, striped bass incidence only varied significantly between the Middle and Inner strata; in this case, more individuals were detected in the Middle region over the study period. These patterns were relatively consistent across years for both species with sturgeon having a broader distribution in autumn-winter months than in spring-summer and striped bass displaying a higher concentration in the Middle stratum during winter that shifted toward the Outer region during spring (Figure 2.4). However, Atlantic sturgeon had somewhat higher incidence during 2018 seasons while striped bass had reduced presence in the Middle stratum during winter and spring the same year.

Environmental drivers of occurrence

The two shallowest receivers were a hot spot for Atlantic sturgeon, especially during spring and summer seasons (Figure 2.5). This hot spot diminished during the autumn, with simultaneous evidence for a cold spot (90% confidence, $p < 0.1$) at the deepest Outer stratum receivers in the same season. During winter, there was an area of increased clustering for Atlantic sturgeon in the deeper section of the Middle stratum and

a significant cold spot (99% confidence, $p < 0.01$) at the deepest sites. Striped bass detection hot spots were only identified within the Middle region. However, clustering occurred at shallower depths during the autumn compared to winter and spring. No striped bass were detected during summer months.

Warmer bottom temperature selection by Atlantic sturgeon and cooler bottom temperature selection by striped bass was a key difference between the two species as they migrated through the study area. Quotient analysis showed that within seasons, Atlantic sturgeon typically tolerated or preferred relatively high bottom temperatures between 9-22°C (Figure 2.6). There was little evidence for temperature selection by sturgeon during autumn, when temperatures mostly occurred within this range. During winter and spring, when temperatures were cooler, Atlantic sturgeon significantly preferred temperatures >11°C. Warmer temperature selection was also apparent during summer, when sturgeon tolerated all temperatures >13°C but selected conditions in the 15-18°C range. In contrast, striped bass significantly avoided temperatures higher than 15°C across seasons. During autumn, striped bass preferred only the coolest available temperatures between 11-14°C. Selection was again relatively narrow in winter months but occurred between 9-13°C, with apparent tolerance for temperatures just outside this range and avoidance of more extreme seasonal bottom temperatures above 14°C or below 7°C. Striped bass broadly tolerated temperatures between 5-12°C in spring months with preference occurring within the 7-8 °C temperature bin. Temperatures higher than 13°C were avoided by striped bass during this season, but wider confidence bands (as a result of low sample size) limit this inference.

Individual migration characteristics

Degree of residency tended to be low for both Atlantic sturgeon and striped bass; average cumulative time spent in the detection radius of receivers per migration season was less than 4 hours for both species (Atlantic sturgeon: mean ± SE = 3.04 ± 0.26 hr; striped bass: 3.25 ± 0.13 hr). Total number of unique days detected for each species were also relatively low across migration seasons (Atlantic sturgeon: mean ± SE = 1.6 ± 0.04 d; striped bass: 2.55 ± 0.05 d). Differences in residency were statistically significant, with striped bass occurring for more hours and days than sturgeon (Wilcoxon rank sum test, hours: $p < 0.001$; days: $p < 0.001$). Striped bass were also detected for more hours and days during autumn/winter months compared to spring/summer months (hours: $p < 0.001$; days: $p < 0.001$). Like striped bass, sturgeon were detected for more days on average during autumn/winter months ($p < 0.001$) but hourly presence did not differ between migration seasons ($p = 0.09$).

Transit rate

Serial detections of striped bass between the coastal MD and DE arrays mostly occurred in the expected direction of movement: south in autumn/winter and north in spring/summer (Figure 2.7). There were occasional instances where individuals made both north and south transits within a migration season (spring 2017: 3 of 38 individuals, autumn 2017: 3 of 33 individuals, autumn 2018: 8 of 23 individuals). Sequential detections between arrays were noticeably reduced during spring of 2018, in which telemetered fish were detected more often in the MD array than the DE array (Figure 2.7). During autumn/winter, mean transit rate in the southerly direction was 0.99 km hr^{-1}

± 0.11 SE and during spring/summer, mean transit rate in the northerly direction was 1.13 km hr^{-1} ± 0.2 SE. Although the fastest observed transit rates (> 2 km hr^{-1}) tended to occur in the northern direction during spring, speed was similar between the two directions of movement ($t = -0.106$, $df = 108.43$, $p = 0.92$). The maximum observed transit rates of 6 km hr^{-1} would translate to 1.7 m s^{-1}, or about two body lengths per second. Each of the best performing models (< 2 Δ AICc) contained TL at tagging as a covariate and all models that included interactions were ranked lower than the null model (Table 2.4). Only TL was found to significantly affect transit rate with larger fish being more likely to transit faster between arrays (Table 4; Sex $p = 0.41$, Season $p < 0.15$, Year $p = 0.29$, TL $p < 0.02$).

Discussion

Comparative migration ecology

In this study, acoustic telemetry and data-sharing allowed me to evaluate and compare the behavior of two species within their migratory flyway. Striped bass and Atlantic sturgeon were transient off the coast of Maryland but differed in their seasonal distribution and use of shelf habitat. Rapid movements through the study area occurred for both species, with evidence that larger striped bass transited at a faster rate than smaller individuals. Relatively few telemetered fish were detected for periods > 24 hr and detection histories were characterized by long periods of absence, particularly for striped bass. Still, multi-day periods of incidence were observed for both species during autumn and winter. Although striped bass were relatively transient during spring months,

individuals were often present for 3 or more days during winter. These results contradict my original hypothesis that the coastal stock of striped bass would rapidly transit through the MAB and suggest some individuals may use this region for overwintering habitat.

When present, Atlantic sturgeon and striped bass preferred distinct habitat gradients; Atlantic sturgeon tended to occur in warmer near-shelf waters while striped bass were more likely to select cooler and deeper areas. However, habitat preference differed seasonally with Atlantic sturgeon having a wider distribution during their fall migration and striped bass selecting deeper waters as near-shelf temperatures rapidly cooled in winter. These seasonal patterns appeared to reflect broader cross-shelf distributional shifts related to depth and temperature gradients rather than selection for specific benthic characteristics. Within the array, hot spots of sturgeon incidence tended to occur over fine sand or mud substrates (Figure 2.1), which aligns with literature reports (Savoy and Pacileo 2003; Stein et al. 2004; Laney et al. 2007). On the other hand, sandy sediments are broadly available to sturgeon across shelf depths in Maryland's coastal habitat, so clustering of detections may reflect response to other environmental conditions that were not evaluated in this study.

The observed patterns of Atlantic sturgeon presence were largely consistent with known aspects of species migration patterns. Tagging and bycatch records in the MAB shelf region have reported the highest numbers of sturgeon captures occurring in the spring and fall (Collins et al. 2000; Stein et al. 2004). Atlantic sturgeon are generally absent from the late spring through early fall, when they are occupying riverine spawning and nearshore foraging habitats (Borodin 1925; Stein et al. 2004). During the winter, sturgeon may be inhabiting relatively warmer habitats to the south, near Virginia and

Cape Hatteras, where they have been shown to aggregate (Moser et al. 1998; Laney et al. 2007; Stein et al. 2004; Dunton et al. 2010). Broader shelf distributions during autumn than during spring and summer have also been observed in landings records, surveys, and electronic tagging studies (Stein et al. 2004; Laney et al. 2007; Erickson et al. 2011; Breece et al. 2017).

In contrast to my original hypothesis that Atlantic sturgeon would slowly transit the study region, movements were relatively quick, with only a few instances (n=15) of seasonal residence ≥ 24 hr. These transit rates may indicate a lack of favorable conditions available for Atlantic sturgeon in the shelf region, although the identified window of temperature selection between 9-22°C is well within the known range of thermal tolerance for this species (Niklitschek and Secor 2009, 2010). The lack of residency by Atlantic sturgeon may instead relate to this shelf region serving mainly as a transit route between northern spawning and nearshore spring/summer feeding grounds and southern winter habitat. Atlantic sturgeon in the coastal ocean are known to concentrate around the mouths of inlets and estuaries in spring, summer, and fall (Dunton et al. 2010; Erickson et al. 2011). Within these regions, sturgeon have been found to associate with river plumes or sandy and muddy substrates that may offer increased foraging opportunities (Savoy and Pacileo, 2003; Laney et al. 2007; Oliver et al. 2013; Breece et al. 2016). This is not to say however, that Atlantic sturgeon did not forage during their occupancy of the study site, where substrate and benthic productivity should support this activity (Dovel and Berggren 1983; Johnson et al. 1997; Woodland and Secor 2013).

Patterns of striped bass occurrence also aligned with established seasonal migrations of south in the fall and north in the spring, but revealed unique patterns of

oceanic incidence in winter and in deeper waters. Striped bass are known to overwinter in the nearshore waters off Cape Hatteras (Chapoton and Sykes 1961; Benton 1992; Laney and Cole 1994), but other portions of the migratory contingent appear to winter in the shelf region as far north as Cape Cod, Massachusetts (Clark 1968; Dorazio et al. 1994; Wirgin et al. 1997; Waldman et al. 2012). My results show that individuals move to areas > 40 km from the coast and occupy the region for an extended period in winter. Peaks in frequency of occurrence during daylight hours may further support the use of Maryland's shelf waters as overwintering habitat for this species; striped bass are predominantly visual predators and could be increasing activity on a diel basis to locate and capture prey. Though striped bass were associated with a relatively narrow range of temperatures, I did identify a lower temperature threshold of 5°C, indicating that striped bass avoid the coldest oceanic temperatures that occur in the near-shelf region during winter. Other fish species in the Northwest Atlantic undertake similar cross-shelf distributional shifts during winter, including black sea bass, fluke (*Paralichthys dentatus*), and scup (*Stenotomus chrysops*) (Nesbit and Neville, 1935; Colvocoresses and Musick, 1984). Like these species, striped bass may select warmer outer shelf waters over the cooler near shelf waters.

Striped bass movement behavior during spring supported my original hypothesis of rapid transit through the MAB shelf region. The highest rates of transit tended to occur in a northerly direction in the spring, corresponding with northward movement toward Delaware and Hudson River spawning areas or summer foraging grounds located off the coast of Massachusetts (Koo 1970; Collette and Klein-MacPhee 2002; Welsh et al. 2007). Spring transits > 4 km hr^{-1} would translate to 1.1 m s^{-1}, or roughly 1-1.5 body lengths s^{-1}

for an 80 cm TL striped bass. Although these speeds are well below maximum sustained swimming speeds of 2.9–3.3 body lengths s^{-1} for striped bass (Freadman 1979), they are greater than mean southern transits, which were closer to 0.3 m s^{-1}, or 1/3 body lengths s^{-1}. Still, uniform directionality was not always observed and sequential detections were not consistent during spring 2018, leading to non-significance in transit speed between the MD and DE arrays. Other telemetry studies have found highly variable rates of transit during spring; some transit intervals between the Delaware Bay and Massachusetts were as rapid as 9 days while other fish stopped for hours to days in bays and estuaries along their migration route (Kneebone et al. 2014). Although striped bass exhibited directed movement in the study area, this does not preclude extended stopovers in the areas like the Delaware Bay, New Jersey estuaries, or Long Island Sound during the spring, which have been recorded in the past (Able and Grothues 2007; Grothues et al. 2009; Kneebone et al. 2014). Consistent with my findings, migration intervals calculated by Kneebone et al. 2014 were, on average, shorter for northward movements of striped bass tagged in Massachusetts. Similarly, Callihan et al. 2015 found that striped bass spawning in the Roanoke River showed directed movements (mean = 0.68 m s^{-1}; maximum = 0.92 m s^{-1}) to northern oceanic regions. Results collectively indicate that striped bass emigrate relatively quickly from southern overwintering and spawning regions, likely motivated by warming temperatures.

Study design

The gradient design, not previously employed in acoustic telemetry studies, provided useful inferences in the comparative migration behavior of striped bass and

Atlantic sturgeon. Telemetry studies often utilize linear receiver gates to assess passage of acoustically-tagged individuals. While gates deployed across geographic bottlenecks provide a high degree of certainty regarding fish presence or absence, these arrangements can also have substantial spatial bias (Krebs 1989; Brownscombe et al. 2019). Studies employing gridded receiver arrays offer a more statistically-robust approach for sampling the environment (i.e. random and uniform) while simultaneously permitting observation over a larger range of habitat types (Kraus et al. 2018). Here, I used a gradient-based extension of the gridded approach to better incorporate hypothesized continuous (gradient) drivers of fish migration. To cover a large shelf gradient, I undertook a sampling rather than a census tactic, the latter requiring ≥100% transmitter detection ranges.

By gathering information across biologically relevant spatial (shelf-wide) and temporal (multi-seasonal) gradients, the study design lent itself to the analysis of species habitat selection (Cushman et al. 2010, Alvarez-Berastegui et al. 2014). For instance, the adjacent DE array, despite potentially higher within-array detection efficiency, recorded far fewer striped bass detections during spring of 2018 (Figure 2.7), likely because it did not extend far enough into deeper shelf waters. Relatively cooler temperatures during the 2018 migration season may have caused striped bass to move faster or farther offshore. Striped bass were almost exclusively detected at Outer receiver sites during this migration season, which contrasted their occurrence across Middle and Outer locations during the spring of 2017 (Figure 2.4). This difference in distribution suggests that the migration corridor for striped bass shifted farther toward the outer shelf in 2018, into a region that was not monitored by the Delaware array. Although wider receiver spacing

and variable detection range may have inflated my assumed absences and led to lower apparent site fidelity, I maintain that these tradeoffs were necessary to understand this segment of the MAB flyway. Still, other designs (i.e., arrangements of receivers) might hold greater advantage depending on whether the purpose was to detect single or multiple species. For instance, a gradient design for sturgeon would be focused more inshore than one for striped bass. Additionally, the latitudinal arrangement of arrays should be revisited against monitoring goals. Here, transit rates within my array were not feasible and required ancillary data from the DE WEA array.

Though the receiver grid comprised a large swath of available cross-shelf habitat, this area represents a small portion of the entire range inhabited by migratory striped bass and sturgeon. My results thus describe a restricted window along an extended migration corridor and inferences may not be applicable to other latitudes of the MAB. Similarly, migration cues likely occur outside the study area. For example, though interannual differences in the wintertime occurrence and cross-shelf distribution for striped bass could be related to measured habitat variables within the study site, the timing and speed of migration probably depends on conditions and seasonal cues occurring in other shelf regions or spawning tributaries such as the Hudson River and Chesapeake Bay. Migratory behavior is often considered preemptive in that individuals will depart areas before they become unfavorable (Dingle and Drake 2007). In the case of estuaries like the Chesapeake Bay, striped bass will emigrate before temperatures become too warm and metabolically demanding, particularly for large individuals > 90 cm TL (Coutant 1985; Hartman and Brandt 1995). However, local habitat attributes still likely influenced patterns of occurrence; striped bass may have transited through the area using deeper

offshore waters during winter and spring of 2018 because they were avoiding excessively cold nearshore temperatures.

Implications

Climate change is now altering marine species distributions in unpredictable ways (Field et al. 2001; Perry et al. 2005; Daskalov et al 2007). Already, poleward shifts have been observed in some northwest Atlantic coastal fishes (Nye et al. 2009; Pinsky et al. 2013). Changes in population response may be particularly complex for species like striped bass and sturgeon that range widely and tolerate a broad range of habitat conditions but also exhibit natal homing to particular estuaries. Based on my results, Atlantic sturgeon may experience an expansion of preferred temperature conditions on the MAB shelf under a warming climate, while striped bass may select deeper habitats to avoid unsuitably warm nearshore waters, particularly during winter. Natal homing for these species to specific estuaries means that climate will drive spatial and temporal migration changes rather than wholesale population shifts in range. Although natal origin of telemetered fish was not considered in this study, my findings demonstrate that gradient designs are well-suited for comparing spatial and temporal differences in species distribution. Similar array designs could be employed to evaluate population-specific shifts in flyway habitat use under changing shelf conditions.

The development of offshore renewable energy infrastructure could also alter coastal migration behaviors within the coming decade. Currently, multiple wind farm installation sites have been leased along the US East coast in areas that coincide with migration corridors. Wind tower construction and site maintenance activities such as pile-

driving, amplified vessel traffic, increased sedimentation, or altered electromagnetic fields caused by power cables could result in physiological stress or avoidance of the area by marine species (Gill 2005; Thomsen et al. 2006; Westberg and Lagenfelt 2008; Boehlert and Gill 2010; Popper and Hastings 2009; Gill et al. 2012). However, within the relatively featureless MAB, added structure from wind turbines may provide habitat throughout the water column and provide refuge or forage resources for both demersal and pelagic fishes (Wilhelmsson et al. 2006; Inger et al. 2009; Bergström et al. 2013). Despite the lack of baseline data prior to construction, recent meta-analyses show that European wind farms harbor higher abundance and diversity of fish species compared to adjacent reference sites (Methratta and Dardick 2019). An altered MAB shelf environment may thus create novel stopover points for previously transient Atlantic sturgeon and striped bass. New traditions of residency or fidelity will be a management concern, as these could eventually shift the extent and timing of species-human interactions.

Coordinated acoustic telemetry arrays using gradient sampling designs, along with increased cooperative data-sharing and analysis, will serve to expand current knowledge on the migration ecology of marine fishes within coastal flyways. Establishing comprehensive baselines will also allow managers and stakeholders to evaluate future impacts of climate change and offshore wind farm development.

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Tables

Table 2.1. List of acoustic transmitters detected in the study area that were provided by co-authors. DSU= Delaware State University; VCU=Virginia Commonwealth University; MA DMF=MA Division of Marine Fisheries; UMCES=University of Maryland Center for Environmental Science; NYS DEC=New York State Department of Environmental Conservation; DE DFW= Delaware Department of Fish and Wildlife.

Species	*PI*	*Institution*	*N*	*Tagging Location*
Atlantic Sturgeon				
	D.A. Fox	DSU	178	Coast of Delaware
	M.T. Balazik	VCU	74	James River
	Others		43	New York, Delaware, Maryland, Virginia, South Carolina
Striped Bass				
	B.I. Gahagan	MA DMF	139	Coastal MA
	D.H. Secor, A.L. Higgs, J.Best	UMCES, NYS DEC	61	Hudson River
	D.H. Secor B.I. Gahagan	UMCES MA DMF	15	Coastal MA
	D.H. Secor	UMCES	13	Potomac River
	I.A. Park	DE DFW	71	Delaware River
	Others		17	New England

Table 2.2. Parameter estimates and best distributions for GARMA models as determined by AIC rankings. Sinhour and coshour refer to transformations of hour-of-day while sinday and cos day refer to transformations of day-of-year. β denotes regression coefficients and φ_j and θ_j are the autoregressive and moving average parameters, respectively. Standard errors are included in parentheses where applicable and significance of parameters are indicated by asterisks (<0.001= ***; 0.001-0.009 =**; 0.01-0.009=*; 0.05-0.1=.).

Parameter	*Atlantic Sturgeon*	*Striped Bass*
Distribution	Zero-Inflated Poisson	Negative Binomial
β intercept	-756.608*** (46.632)	-557.196*** (84.026)
β sinhour		477.956*** (36.099)
β coshour		-248.956*** (50.301)
β sinday	249.633*** (22.337)	0.149*** (0.043)
β cosday	233.368*** (26.547)	-0.103* (0.041)
θ_1	0.491*** (0.022)	-0.453*** (0.018)
θ_2	-0.437*** (0.026)	-0.156*** (0.017)
θ_3	-0.11*** (0.023)	-0.06*** (0.016)
φ_1	0.155	1.0
φ_2	0.843	

Table 2.3. Statistical results from Kruskal-Wallis (K-W) and Dunn's post-hoc tests on how number of individuals detected vary between seasons and strata. Asterisks indicate statistical significance.

Species		*K-W*		*Dunn's test*			*K-W*		*Dunn's test*	
		X_2	*p*	*z*	*p*		X_2	*p*	*z*	*p*
Atlantic Sturgeon	**Season**	42.85	<0.001*			**Stratum**	52.27	<0.001*		
	Autumn-Spring			4.257	<0.001*	Inner-Middle			3.234	0.002*
	Autumn-Summer			6.253	<0.001*	Inner-Outer			7.092	<0.001*
	Autumn-Winter			3.120	0.006*	Middle-Outer			5.452	<0.001*
	Spring-Summer			1.822	0.205					
	Spring-Winter			-1.473	0.420					
	Summer-Winter			-3.471	0.002*					
Striped Bass	**Season**	86.20	<0.001*			**Stratum**	8.949	0.01*		
	Autumn-Spring			-3.689	<0.001*	Inner-Middle			-2.863	0.006*
	Autumn-Summer			3.266	0.003*	Inner-Outer			-1.068	0.429
	Autumn-Winter			-5.856	<0.001*	Middle-Outer			1.555	0.198
	Spring-Summer			6.349	<0.001*					
	Spring-Winter			-1.549	0.364					
	Summer-Winter			-8.504	<0.001*					

Table 2.4. Linear mixed model results and model factors for the top 5 models for log-transformed striped bass transit rate (Log km hr^{-1}) including Tag ID as a random effect (1 | Tag) to account for repeated measures. TL= Total length at tagging in cm. AICc = corrected Akaike's Information Criterion; LogLik = Log Likelihood.

Model	*df*	*AICc*	*Δ AICc*	*LogLik*
Log km hr^{-1} ~ TL + (1 | Tag)	4	230.5	0.00	-110.992
Log km hr^{-1} ~ Season + TL + (1 | Tag)	5	231.5	1.07	-110.403
Log km hr^{-1} ~ Year + TL + (1 | Tag)	5	232.0	1.57	-110.654
Log km hr^{-1} ~ Sex+ TL + (1 | Tag)	5	232.5	2.02	-110.882
Log km hr^{-1} ~ 1 + (1 | Tag)	3	233.5	3.03	-113.600

Figures

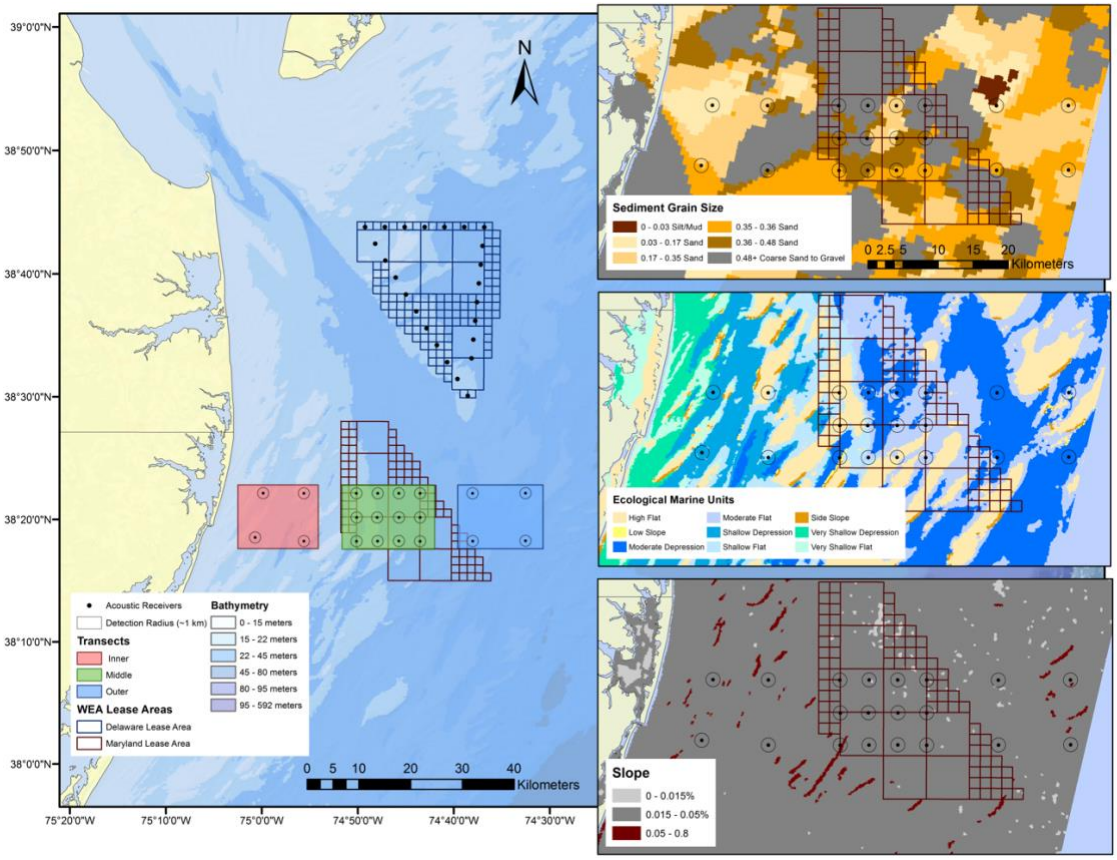

Figure 2.1. Map of study region including acoustic receiver array design and benthic habitat features. Maryland and Delaware Wind Energy Areas with respective receiver locations and depth contours are shown. Inset panels depict sediment and topography characteristics within the study array off the coast of Maryland. Ecological Marine Units (middle inset panel) represent a three-way combination of depth, sediment grain-size, and seabed forms that were found to influence ecological relationships of surveyed organism communities (Source: Northwest Atlantic Marine Ecoregional Assessment, The Nature Conservancy).

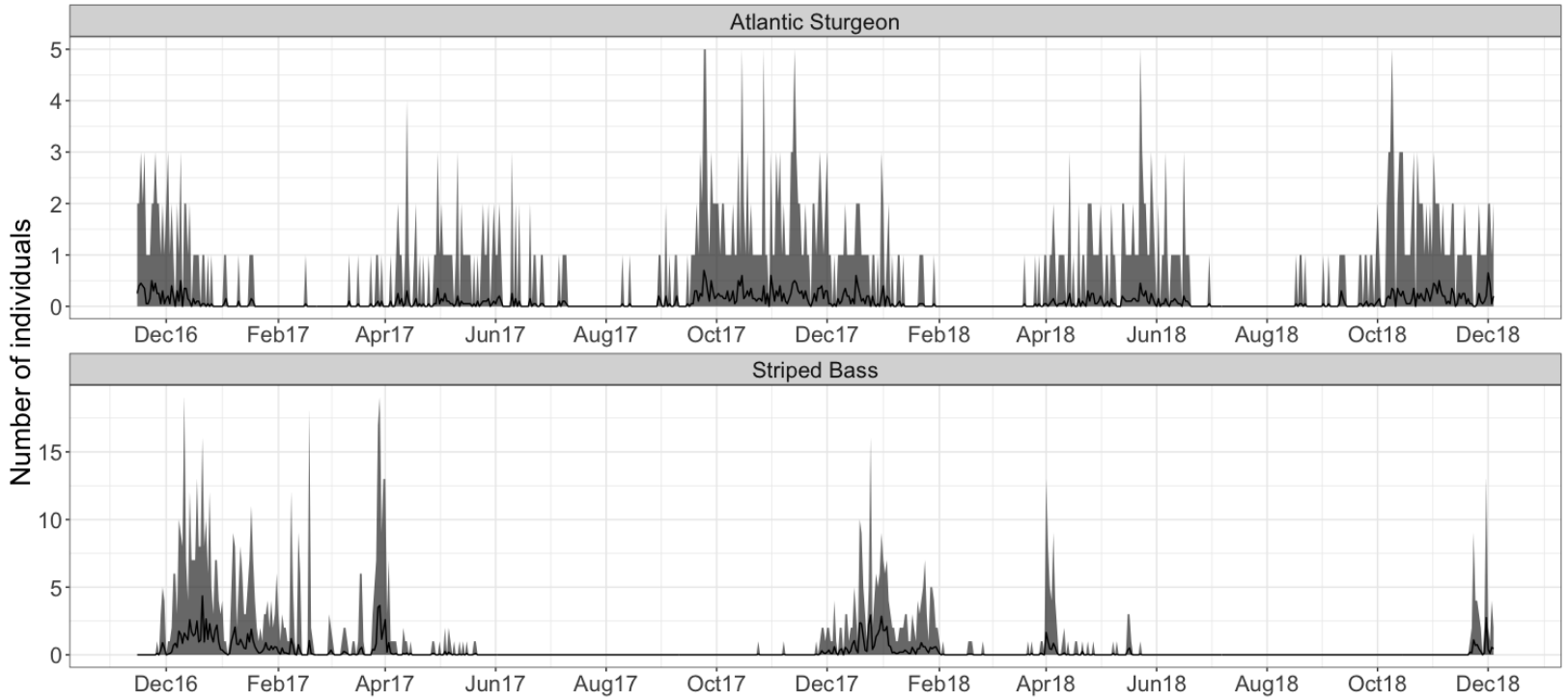

Figure 2.2. Number of unique individual Atlantic sturgeon (top) and striped bass (bottom) recorded per receiver, summed per day. Gray shading represents the minimum and maximum values of incidence across the array. Black lines show the mean number of individuals detected across the array. Note the differing scales on the y-axis.

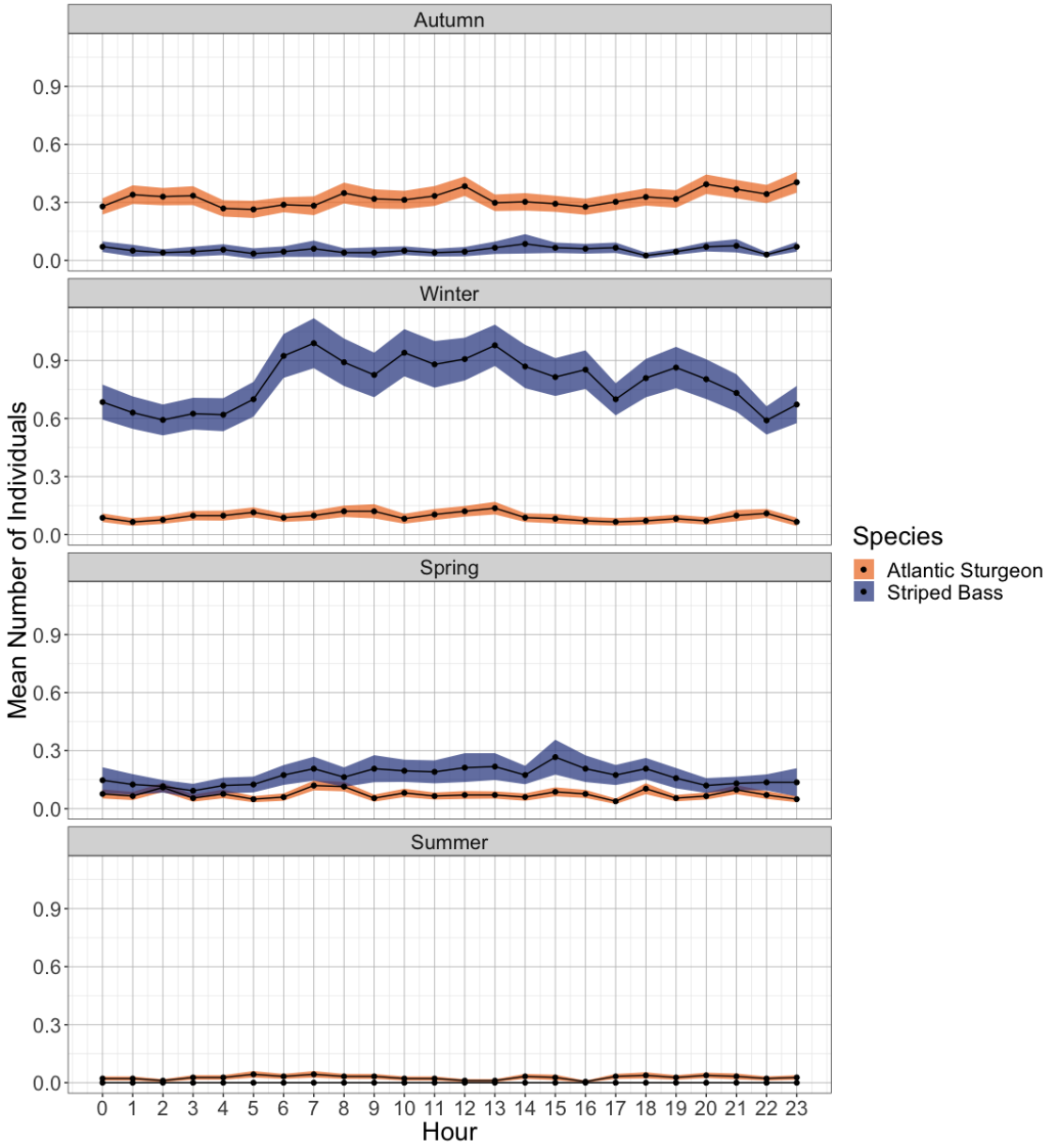

Figure 2.3. Hourly mean number of unique individual fish detected between November 2016 and December 2018. Shaded bands represent the standard error.

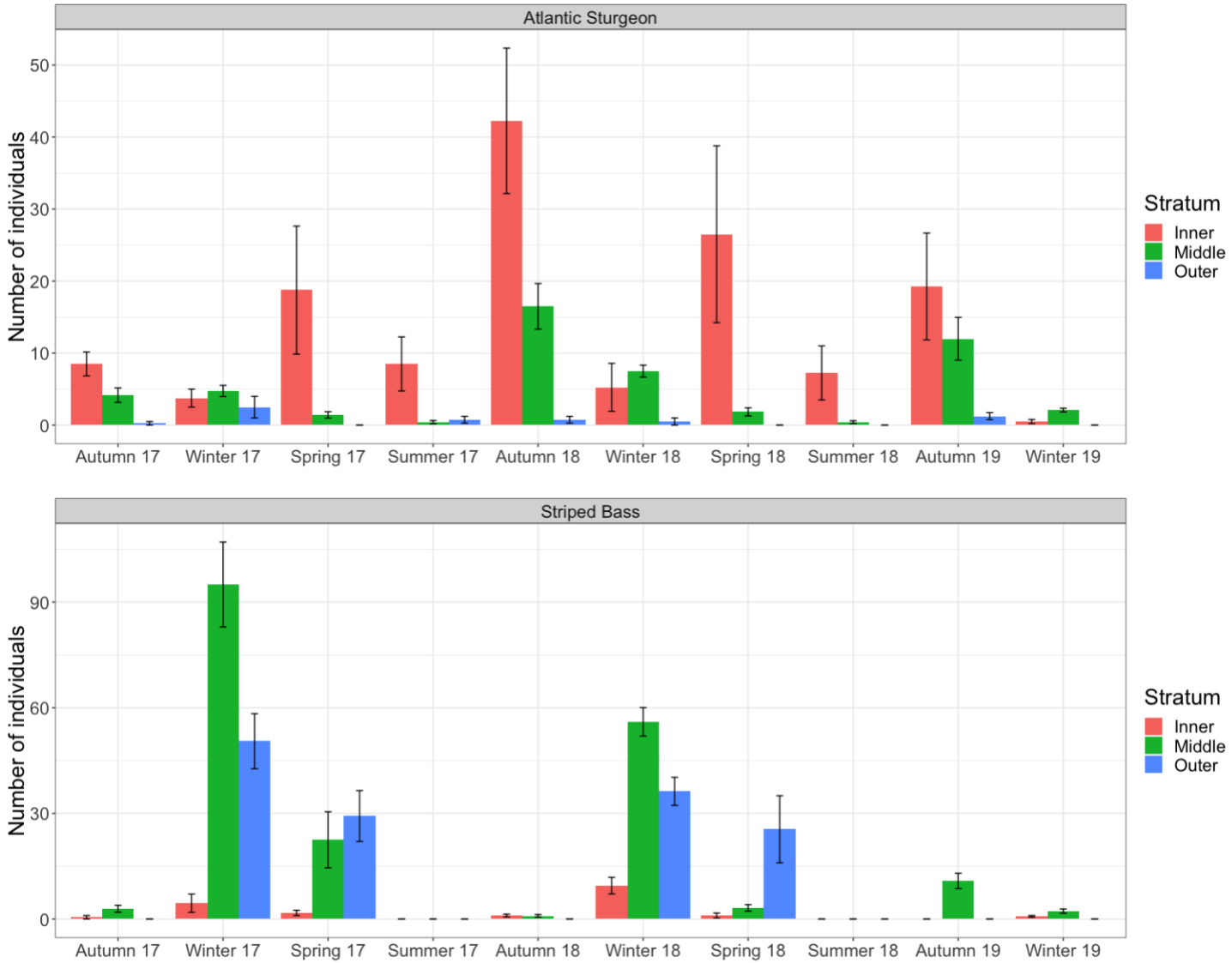

Figure 2.4. Mean ± standard error number of individual Atlantic sturgeon (top) and striped bass (bottom) detected by receivers within each stratum and Season/year.

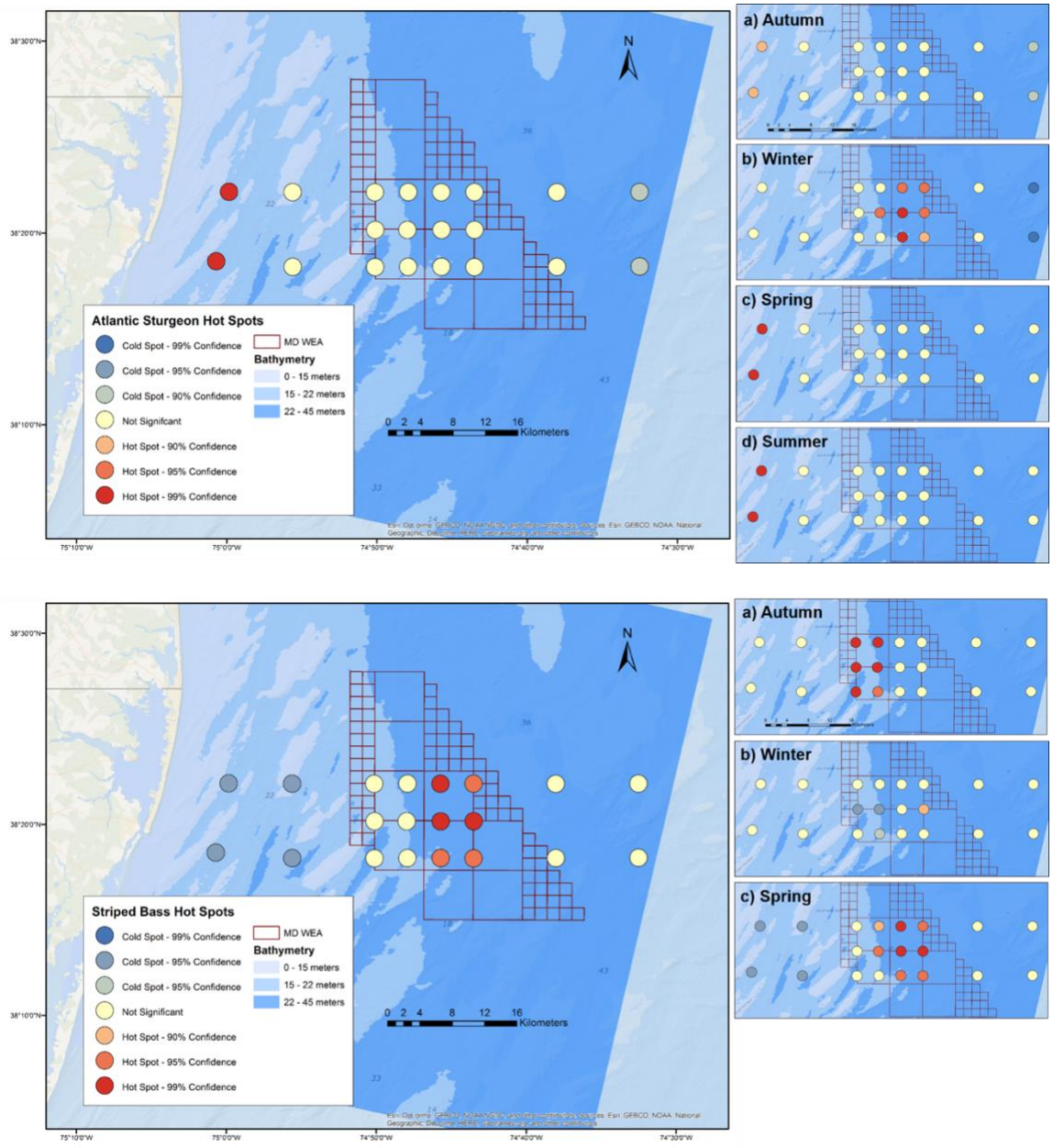

Figure 2.5. Results of Hot Spot analysis for annual (left) and seasonal (insets, right) numbers of individual Atlantic sturgeon (top) and striped bass (bottom) detected per receiver.

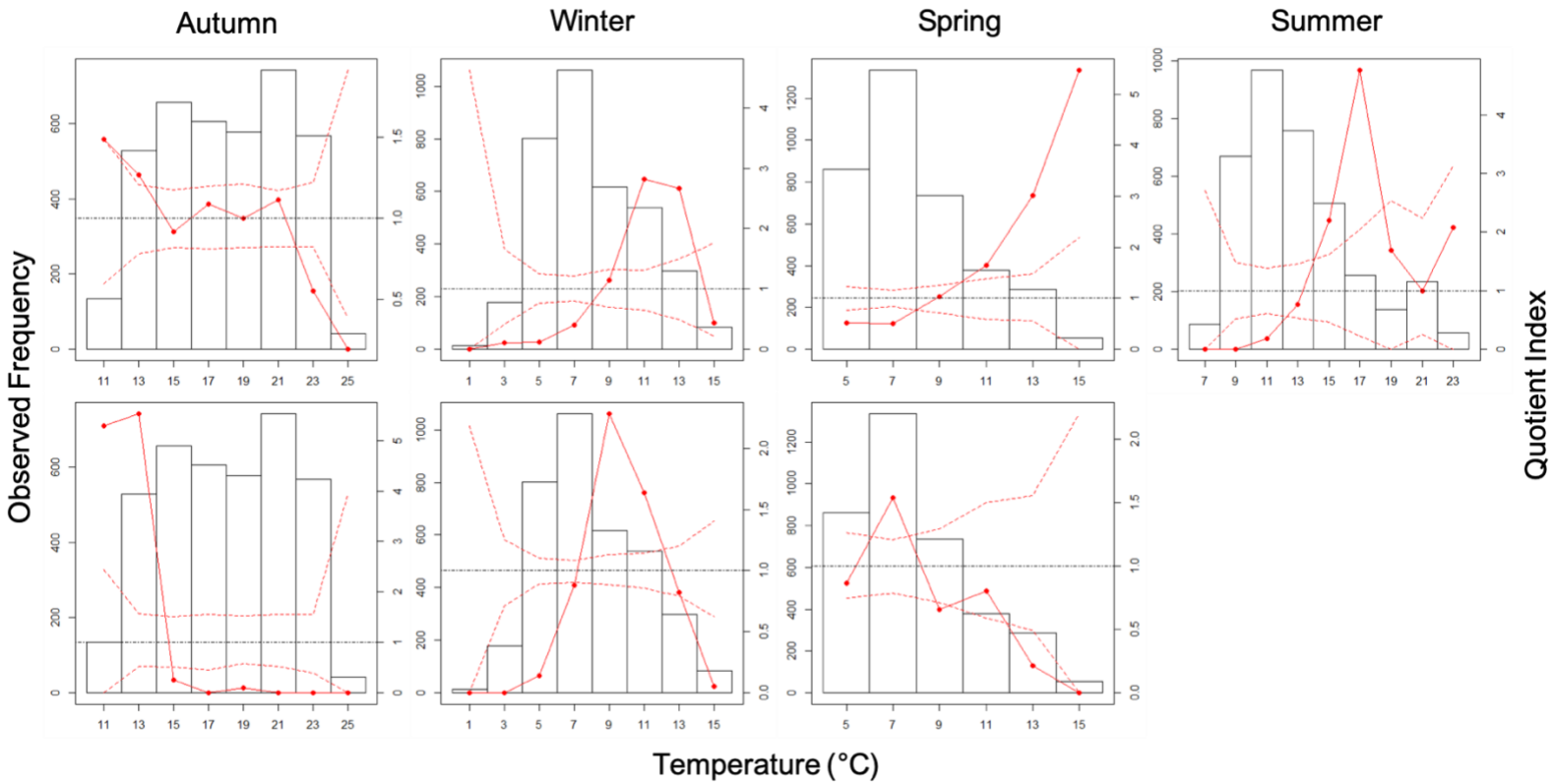

Figure 2.6. Quotient analysis plots for temperature preference of Atlantic sturgeon (top) and striped bass (bottom) across seasons. Each plot shows the observed quotient index (QI) curve (solid red line), its confidence interval (dashed red lines), and the frequency histogram of bottom temperature. Points within the confidence band represent tolerance for temperature conditions while points above the band suggest selection and points below the band indicate avoidance. The dotted black line in each plot indicates the value QI=1.

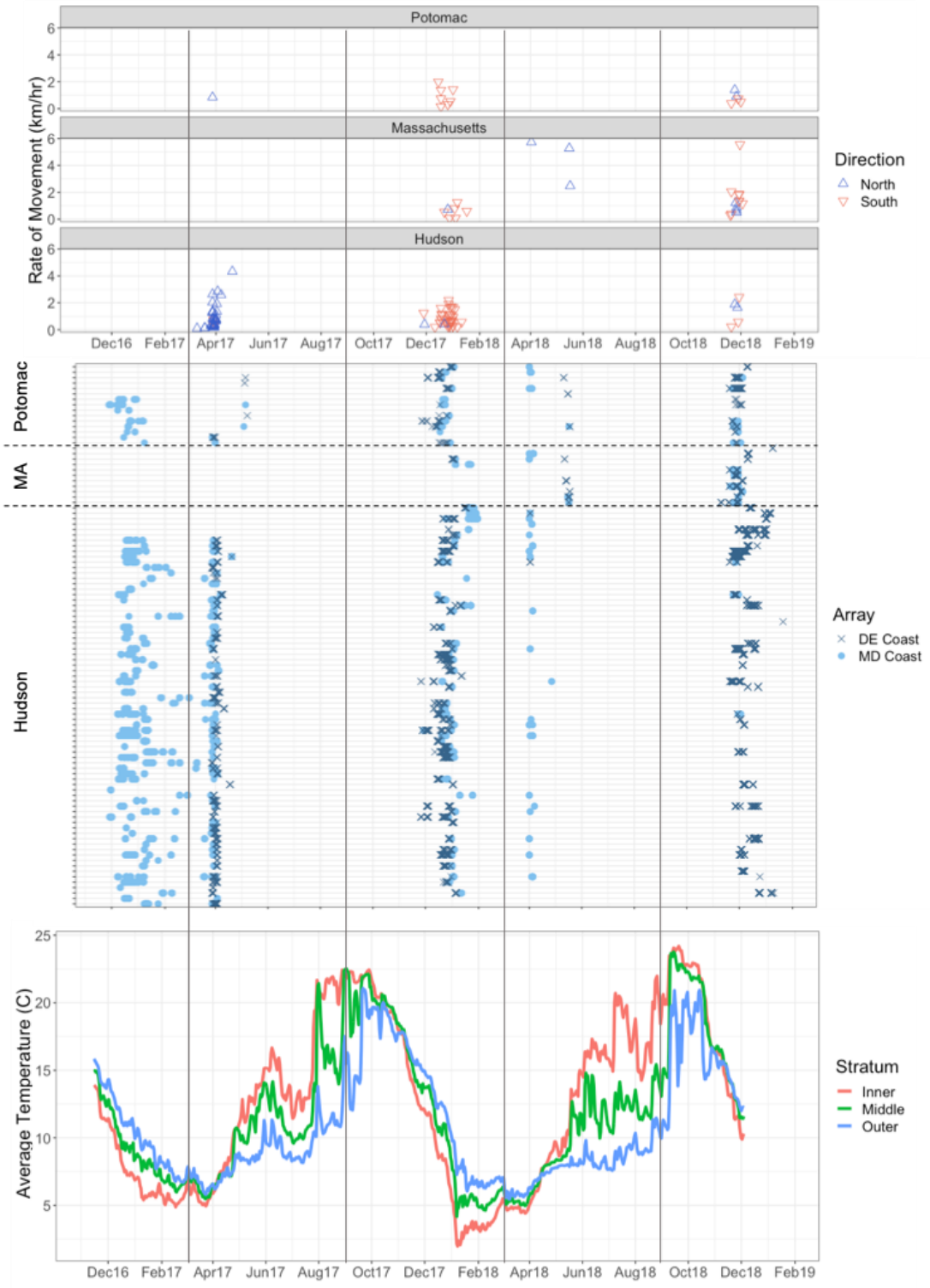

Figure 2.7. Summary of transit information for striped bass by tagging region from November 2016 - December 2018 including transit rate of movement (top panel), timing of detection for acoustically-tagged individuals (middle panel), and average bottom temperature recorded by receivers (bottom panel).

Chapter 3: Environmental and individual drivers of Atlantic sturgeon and striped bass occurrence in the Maryland Wind Energy Area

Introduction

The development of offshore renewable wind energy infrastructure poses an imminent concern to fisheries management in large shelf regions where evaluating and monitoring fish behavior is inherently challenging. Construction and maintenance of wind power facilities in the shelf environment will have both negative and positive impacts in shelf ecosystems (Boehlert and Gill 2010; Bailey et al. 2014; Methratta and Dardick 2019). Disturbances such as pile-driving and increased vessel traffic may lead to physiological stress, avoidance, or evacuation of the area by marine organisms (Thomsen et al. 2006; Popper and Hastings 2009; Gill et al. 2012). However, some long-term effects could be beneficial: wind turbine structures have been known to promote the settlement of invertebrate communities, which provide forage for fish and could cause mobile predators to dwell in the region, thus altering their movement patterns and enhancing local fisheries (Inger et al. 2009; Andersson and Ohman 2010; Langhamer 2012; Bergström et al. 2013). The potential impacts of wind energy development on marine fishes are therefore likely to shift over phases of construction and operation and depend on when and how species currently utilize shelf habitat.

The leased Maryland Wind Energy Area (MD WEA) is located 20-40 km off the coast of Maryland (Figure 3.1) and could consist of >100 turbines (DOI 2014). Although ecological impacts were a central consideration in siting design (McCann

2012; Petruny-Parker et al. 2015), this area overlaps with habitat used by multiple species of economic or conservation importance. Construction time frames and longer-term impacts following tower installation must comply with government standards that limit harmful effects on commercially important species and species of concern as mandated by the US National Environmental Policy Act, the US Endangered Species Act, and the US Magnuson-Stevens Fishery Conservation and Management Act. Thus, to effectively mitigate harmful impacts to fisheries and species of concern, the current seasonal distribution and habitat use of critical fish species in the affected shelf region should be well understood so that future changes in behavior can be evaluated.

Migratory species present a particular challenge in understanding and mitigating impacts of offshore wind development. Though often only transient in a given shelf region, migratory marine fish rely on such regions as transit routes between the spawning and foraging habitats that are essential to population persistence (Able 2005; Secor 2015; Dunn et al. 2019). Atlantic sturgeon and striped bass are two representative species of management concern that seasonally migrate through Northwest Atlantic coastal waters but differ in their spatiotemporal use of the shelf environment (see Chapter 2). In the MD WEA, the focus of this study, Atlantic sturgeon traverse through the Area for extended periods during autumn and spring while striped bass rapidly migrate through during spring and then have slower rates of transit during winter. Further, Atlantic sturgeon tend to occupy shallower near-shelf waters and warmer bottom temperatures while striped bass are more likely to be present at greater depths and in comparatively cool bottom temperatures (see Chapter

2). Thus, the presence of these two species depends on complex responses to seasonal cues and environmental conditions in the MD WEA and the broader MAB. Further, these species represent a mix of population and individual attributes that may also affect their patterns of occurrence in the MAB.

Improvements in biotelemetry present a timely opportunity to describe and predict the presence of migratory species in Maryland's shelf waters (Heupel et al. 2006; Donaldson et al. 2014; Hussey et al. 2015). Unlike traditional mark-recapture or survey methods, acoustic telemetry allows for the long-term, repeated monitoring of acoustically-tagged individuals (Secor 2015). Additionally, acoustic release-enabled receivers facilitate the long-term deployment of surveying devices within remote areas that are often difficult or expensive to access. Measures of species incidence can then be coupled with environmental variables, measured either directly from receivers and other in-situ sensors, or obtained from remote-sensing satellites (Hidalgo et al. 2016). Once data are collected, species distribution modeling techniques can be used to examine the complex relationships between environmental predictors and species presence. Certain approaches, such as Generalized Additive Modeling, (GAM; Wood 2017) allow for flexible modeling of skewed response variables that are expected to vary non-linearly with predictors, as is common in habitat selection modeling (Barry and Welsh 2002). Together, these methods can be used to develop explanatory and predictive tools to inform species management and limit harmful anthropogenic impacts such as those associated with wind farm development and increased vessel traffic (Turner et al. 2017; Hazen et al. 2017; Breece et al. 2018).

To accurately measure or predict migratory species distribution in shelf ecosystems, environmental conditions must be measured over long time periods at the same daily resolution and large spatial extent that individual fish experience the marine environment (Scales at al. 2017; Kavenaugh et al. 2016; Schneider 2017). Long-term, gradient-based designs present a possible solution to this sampling challenge. With a gradient approach, acoustic receivers can sample large swaths of the shelf ecosystem, transecting migration corridors. Although more closely spaced (<1 km) receivers can provide full censusing of shelf regions, owing to expense and logistics such regions are typically quite small compared to the scale of transit habitats. Rather, sampling over a broad environmental gradient provides better context for the range of variables individuals may either select or avoid as they migrate (Kraus et al. 2018). The accuracy and relevance of habitat selection models for striped bass and sturgeon thus depends on collecting information across the full range of conditions available during their presence on the shelf.

The complex life history and population characteristics of migratory species introduce additional complications to evaluating the behavior of Atlantic sturgeon and striped bass in Maryland's shelf waters. Shelf groups of both species comprise multiple populations that originate among several Mid-Atlantic estuaries. Like salmon species, shelf migration pathways could vary by population (Crossin et al. 2007; Hanson et al. 2008; Rogers and Schindler 2008). The US Atlantic sturgeon population consists of five distinct population segments (DPSs) that may be expected to differ in terms of timing of arrival and behavior in the MD WEA region (ASMFC 2017). Similarly, coastal striped bass in the MAB mostly originate from either the

Hudson River, Delaware Bay or Chesapeake Bay estuaries (Wirgin et al 1997; Kneebone et al. 2014; ASMFC 2016). Further, data sharing agreements limited individual fish data to which I had access. Thus, I had incomplete information on species size, sex, and genetic origin. For striped bass location of tagging was often informative of population of origin because much of the tagging occurred on spawning runs. This was not the case for Atlantic sturgeon, where most tagging occurred in shelf regions or estuaries where mixed populations occur (Dunton et al. 2012; Wirgin et al. 2015a; b). Still, location of tagging was retained for both species as a variable of interest related to past group migration behaviors. Despite the lack of true population data, variation in group-level migration patterns could have implications for management.

Here, I test environmental and species population explanatory variables to predict the incidence of Atlantic sturgeon and striped bass at scales that are relevant to future wind energy development and its impact in the MD WEA. Previous results and past habitat-selection modeling in the Mid-Atlantic suggest that variables such as sea surface temperature, bottom temperature, depth, and oceanographic satellite-derived measures of productivity will be important drivers of species presence (Manderson et al. 2011; Breece et al. 2017; Haulsee et al. 2018; see Chapter 2). Focused Atlantic and green sturgeon habitat selection studies have revealed significant effects of bottom type and topography on fish distribution (Stein et al. 2004; Huff et al. 2011), but hotspot analysis in the MD WEA did not support the importance of specific benthic variables (see Chapter 2, Figure 2.5). I therefore focused on area-specific oceanographic conditions and bathymetric gradients for

analyses. I also expected that species occurrence would be influenced by broader regional magnitude of sea surface temperature change over the recent past (e.g. Reyier et al. 2014), and depend on the tagging origin of individuals. A sampling approach allowed me to gather information over relevant time scales along key habitat gradients. GAM formulations were then used to adjust for spatiotemporal autocorrelation and group-based heterogeneity through random effects and hierarchical fixed effect structures (Bolker et al. 2009). Further, I weighted analysis by detection efficiency of acoustic tags, which varied with ambient noise (principally surface winds), by modeling receiver detection efficiencies, which varied both seasonally and sub-regionally within the study array. Detection efficiency was measured during a concurrent field test over a one-year period in the MD WEA (Secor et al. 2019a) and used to derive an index of detection for each receiver.

The present study utilizes a sampling-based approach to evaluate and predict the relative abundance, occupancy, and timing of migratory species in the MD WEA and adjacent shelf waters. My objective was to develop useful predictive models of Atlantic sturgeon and striped bass incidence that can address government agency and wind energy developer needs to inventory these species in plans of wind tower siting and construction. First, I sought to construct a dynamic model of relative abundance to predict spatial and temporal density of Atlantic sturgeon and striped bass. Second, I evaluated the amount of time that species and populations spent in the region depending on environmental conditions. Sampling assumptions differed between these objectives and associated scales of response, so three unique modeling structures were employed (Table 3.1). Resulting models provided forecasts of when

and where migratory striped bass and sturgeon occurred within the MD WEA to inform both decisions on offshore wind farm construction and future evaluations of the potential long-term effects caused by these installations.

Methods

Acoustic telemetry array and transmitters

The occurrence of Atlantic sturgeon and striped bass was monitored in the Maryland shelf region using acoustic telemetry. Owing to priorities related to recovery (Atlantic sturgeon) or management (striped bass), these species currently comprise the vast majority of acoustically-tagged fish in the MAB (see Chapter 2; Table 2.1). An array of 20 acoustic-release (VEMCO © VR2AR) receivers was deployed to detect the presence of sturgeon and striped bass that had been tagged with acoustic transmitters. To accommodate gradient-based sampling, yet retain an emphasis on movements within the MD WEA, the main receiver array was focused within the proposed MD WEA, but sets of receivers were placed both inshore and offshore at set distances (Figure 3.1). The main MD WEA stratum of 12 receivers was located within the footprint of the proposed MD WEA with receivers spaced at 3.2 km and 3.6 km intervals respectively in East-West and North-South directions. The Inner and Outer strata were located 8 km inshore and offshore of the MD WEA stratum and consisted of four receivers at 8 km spacing in both directions. Although detection probabilities were substantially lower in the Inner and Outer strata compared to the MD WEA stratum, total receiver coverage across the shelf region

permitted the analysis of sturgeon and striped bass detections from 10-50 km offshore and 10-45 m depth.

Seasonal and inter-annual variation in migration behavior was studied during a two-year period. From November 2016 – December 2018, each bottom-moored receiver recorded bottom temperature (°C) and non-calibrated, relative ambient noise at the 69 kHz level (mV) at hourly intervals (see Chapter 2 for details on mooring). Detections of unique transmitter codes were logged on a continuous basis. Data were downloaded during tri-annual maintenance cruises. Detected codes were matched with species and tagging information provided by data-sharing agreements and the regional Atlantic Cooperative Telemetry (ACT) Network. Cooperative agreements facilitated the potential detection of >500 striped bass and nearly 1000 Atlantic sturgeon tagged with active acoustic transmitters during the period of array deployment (Secor et al. 2019a)

Detection efficiency adjustments

In a related study (Secor et al. 2019a), seasonal and environmental effects on VR2AR detection range were quantified and modeled in a field test concurrent to the array deployment. Testing took place at both a shallow Inner stratum site and a relatively deeper Middle stratum site (Figure 3.1). Each range test consisted of two synchronization receivers: one deployed at 250 m and one at 800 m. These fixed ranges allowed for analysis of daily detection rates at 250, 550, and 800 m distances. Detection at the 550 m range was quantified using detection rates between the receivers deployed at 250 and 800 m. Daily frequency of detection was calculated per

distance (250 m, 550 m, 800 m) and per site. The proportional daily detection was calculated as

$$\frac{transmissions_{ij}}{transmissions_{i}}$$

where $transmissions_{ij}$ are the transmissions from receiver i detected at distance j and $transmissions_{i}$ are the total transmissions from receiver i. The 50th percentile detection efficacy (D50) was estimated for each day using a binomial regression with a logit link function. These in turn were used in a GAM predictive model that included terms for receiver-recorded absolute noise at the 69 kHz level, bottom temperature, and ΔT (SST from satellite data- bottom temperature recorded by recievers). Since receivers were moored 1 m from the seafloor, their in-situ temperature measurements were considered a satisfactory approximation of bottom temperature. The fitted GAM included singular smooth terms for ΔT and noise as well as an interaction between these two terms (deviance explained = 82.6%, adj. R^2 = 0.85). Larger ΔT values (stratification) were found to increase detection distance and D50 decreased as ambient noise increased. Site-specific D50 as predicted from the final range test model, which ranged from ~ 10-1100 m, was added as an offset to the GAMM habitat models. This predicted range represented an index of sampling effort and was used to adjust each day's sum of detections such that abundance recorded on days with lower D50 values were up-weighted and abundance recorded on days with larger detection ranges were down-weighted. The D50 offset thus

reduced temporal autocorrelation caused by underlying fluctuations in detectability. Details of range test modeling procedures can be found in Secor et al. (2019a).

Environmental data

Environmental and oceanographic variables were obtained from a combination of receiver and remote sensing data sources. Daily average bottom temperature and ambient noise at 69 kHz was calculated using logged VR2AR receiver data recorded on an hourly basis, while daily, satellite-measured, blended sea surface temperature (SST) was accessed via the CoastWatch West Coast Regional Node ERDDAP server (https://coastwatch.pfeg.noaa.gov/erddap/; dataset ID jplMURSST41). Eight-day average chlorophyll-a (CHL-A) concentrations recorded by the MODIS-aqua satellite were also obtained from the ERDDAP server (dataset ID erdMH1chla8day). Although a daily resolution would have been preferable, cloud cover prevented matches for nearly 80% of the daily detection events. Averaging over 8 days allowed us to retain 90% of the detection dataset. Approximate receiver-based bathymetry was calculated from the NOAA Coastal Relief Model available on the ERDDAP server (dataset ID usgsCeCrm2) by downloading data surrounding a 0.1 km radius centered on each receiver and averaging to create a depth value for each location. The difference between satellite-observed SST and receiver-recorded bottom temperature (ΔT) was used as an index of water column temperature stratification; higher absolute values of ΔT represent increased stratification strength. Magnitude of monthly SST change was calculated using the difference between

current SST on a given day minus the lagged SST value over the previous 1-30 days (SST Δ1-30).

Relative abundance model formulation, selection, and evaluation

Daily relative abundance of each species was predicted through a generalized additive mixed model (GAMM) (Table 3.1). All modeling was conducted in R statistical software (R Development Core Team, 2015) using the mgcv package (Wood and Wood 2019). The response variable, daily individual incidence, was calculated by tallying the total number of unique tag codes (individual fish) detected at each receiver, each day. The skewed and over-dispersed data was modeled using a zero-inflated Poisson distribution. Receiver site and study year were added as random effects to limit spatial autocorrelation and to account for inter-annual differences in the number of fish detected.

Bottom water temperature, SST, stratification (ΔT), magnitude of warming or cooling trends (SST Δ1-30), bathymetry, and CHL-A were considered as potential environmental covariates. Preliminary examination of collinearity through pairwise comparison and variance inflation factor calculation showed that SST, ΔT, and bottom temperature were highly correlated ($r > 0.7$, variance inflation factor > 3). SST was selected among these variables because it was most accessible via the ERDDAP server. Similarly, SST Δ1-30 was strongly correlated with SST; here models included either but not both variables. To account for seasonality in the data, day-of-year (DOY) was included as a predictor variable. The oscillatory nature of DOY was accommodated using cyclic splines (bs= “cs”; gam function, mgcv

package) (Wood 2017). All other variables were modeled using singular smooth terms (formula= s, gam function, mgcv package) and thin plate regression splines (bs= “ts”, gam function, mgcv package) and were limited to 6 knots to reduce potential over-fitting (Wood, 2003). Interactions between environmental variables and DOY were also systematically included and a tensor product smooth term (formula= t2, gam function, mgcv package) was used to account for differing units among interaction variables (Wood et al. 2013). Only one interaction was allowed per modeling iteration to limit complexity.

All possible relative abundance model combinations were tested and ranked according to AIC score. Final models were then checked for concurvity, the non-linear equivalent of collinearity using the “concurvity” function in the mgcv package. Concurvity occurs when there is similarity between the smooth functions of different variables. Concurvity can thus lead to difficulty in interpreting model effects and in severe cases can bias estimates of residual variance, leading to false confidence in results (Ramsay et al. 2003). Therefore, if observed values of concurvity were > 0.8 (values range 0-1, with higher values indicating increased concurvity), the model was dismissed from consideration. Since SST and SST Δ24-30 always resulted in concurvity values exceeding 0.8, only models that included SST Δ1-23 were used for selection. Final model residuals were visually checked for temporal and spatial correlation using autocorrelation function (ACF), partial autocorrelation function (PACF), and semi-variogram plots. Overall model performance was evaluated with k-fold cross validation in which the data were randomly split into training (75%) and testing (25%) sets over each of 5 folds. The root mean square error (RMSE) and

average error between observed abundance in testing data and training model-predicted abundance were then calculated and used to assess model predictive error (Potts & Elith 2006).

Environmental and individual drivers of residency

Environmental drivers of individual residency on the MAB shelf were also assessed using a zero-inflated GAMM approach (Table 3.1). The response variable for residency models was the total number of days of positive detections within each week. Individual ID (transmitter code) was included as a random effect to account for correlation from repeated measures of the same individual. "Population"-level differences in individual response were tested in the same model by considering tagging region as a fixed effect. Only tagging regions with a sample size > 5 individuals were included in analyses. Differences between tagging regions was evaluated using the *post-hoc* multiple comparison, Wald test (wald_gam function, 'itsadug' package; Van Reij et al. 2017).

Week-of-year, CHL-A, and SST were examined for their effect on the weekly residency of individual fish. Thin plate splines with a limit of 6 knots were used to specify all environmental covariate functions with the exception of week-of-year, which was modeled with a cyclic spline. Although models likely suffered from concurvity, thus increasing the potential for biased estimates or Type I error (Amodio et al 2014), SST and week-of-year were both retained so that the influence of each term could be evaluated while accounting for individual-level variability.

Preliminary analysis showed that inclusion of individual random effects did not resolve all residual temporal autocorrelation and unlike daily-resolution modeling, the use of a D50 offset did not effectively diminish correlation at the weekly timescale. A state-dependence approach using lagged individual residency was used to model and reduce remaining serial autocorrelation in weekly residence probability. Three state-dependence sub-models were created that corresponded to how many days an individual fish was detected in the previous 1-3 weeks. Each considered submodel added the first- through third-order smoothed autocorrelation terms to find which structure most decreased autocorrelation while limiting complexity. Residual autocorrelation was again checked using ACF and PACF plots. Residual spatial correlation was not a concern in this analysis because residency was modeled over the entire array.

Population-level differences in residency response

When significant differences in residency were identified between tagging regions (populations) in the GAMM *post-hoc* tests described in the previous section, hierarchical generalized linear models, or HGAMS, were used to further evaluate the group-level differences in response to environmental and temporal covariates (Table 3.1). HGAMs are used to allow for varying degrees of non-linear response over different grouping levels (Pedersen et al 2018). For hierarchical modeling, significant predictors of residency were each tested individually. The smoothed functional response in each model was allowed to vary by group (tagging region), but group-level functions were pooled in a common response. The hierarchical relationship

between predictor variables and tagging-region groupings was specified using different variable and factor relationships. First, the global response of all groups to the variable of interest (either week-of-year, SST, or CHL-A) was specified using a singular thin plate regression spline. Next, the predictor was modeled according to each tagging group factor using the factor-by-smooth model specification (formula = "by", gam function, mgcv package). However, a cyclic spline was still used to model the temporal week-of-year variable. Finally, a random effect for tagging group was explicitly included so that model intercepts could differ among the group factor levels (Pedersen et al 2018). Collinearity between the global response and group-level responses was deliberately penalized and reduced using additional model terms (bs= "ts"; m=2, gam function, mgcv package), thereby increasing certainty around the global smoothed predictor (Wieling et al. 2016; Baayen et al. 2018). The best state-dependence correlation structure identified in the full residency model was used in hierarchical models. Model diagnostics and performance were not assessed for HGAMs since they were intended to visualize the group-level differences in response to individual environmental covariates and not to predict residency.

Results

Relative abundance model selection

A total of 753 potential predictive models were considered for each species. For Atlantic sturgeon, the top 10 models all contained an interaction between depth and DOY (Table 3.2). The top three ranked models all included significant effects of

CHL-A, the interaction between DOY and depth, and the magnitude of SST change over the previous 3-4 days. AIC scores and deviance explained were similar among these three models (<Δ2 AIC; <Δ1% deviance explained), but the model containing a smooth for SST Δ4 d had the best overall performance and was selected as the best fitted GAMM.

For striped bass, the interaction between depth and DOY was also retained in the 10 best models (Table 3.2). However, in contrast to the importance of SST change on the 3-4 day timescale identified in Atlantic sturgeon models, the top ranked models for striped bass showed that abundance was more likely to be affected by the magnitude of SST change over the previous 15-20 days. Though top-ranked striped bass GAMs explained a similar amount of deviance (<Δ2% deviance explained), the best model, which contained a significant effect of SST Δ17, resulted in an AIC score that was substantially lower than the next best model (>Δ10 AIC).

Atlantic sturgeon relative abundance results

The best predictive model for Atlantic sturgeon revealed a bimodal response to the magnitude of SST change over the previous 4 days; individuals were most likely to occur when surface temperature had decreased ~ 2.5°C or when it had increased more rapidly, by up to 4°C (Figure 3.2). Greater abundance of Atlantic sturgeon was also more likely at lower CHL-A concentrations with a peak in predicted occurrence just above a concentration of 5 mg m^{-3}. Atlantic sturgeon exhibited a complex response to depth in which individuals were more likely to occur at shallow depths (< 20 m) during the spring but were more broadly distributed across

mid-range and shallow depths (~15-35 m) during autumn and winter (Figure 3.3). The 5-fold cross-validation RMSE of the model was 0.29 ± 0.01 and average error was -0.001 ± 0.004, meaning the model-predicted abundance was 0.06 of the maximum number of sturgeon per receiver deployed (maximum =5) with an error <0.01 of the maximum and thus error was small compared to the units of individual incidence. Model diagnostics did not show spatial or temporal autocorrelation in residuals (Appendix, Figure A.1; A.2).

Striped bass relative abundance results

The selected GAMM for striped bass predicted the highest number of individuals when SST had decreased ~ 4°C or increased more than 4°C over the preceding 17 days (Figure 3.4). Higher striped bass abundance was also likely when SST had remained relatively constant (Δ0) over 17 days. Striped bass had increased likelihood of occurrence as CHL-A concentration increased. Like Atlantic sturgeon, striped bass abundance varied spatially over the DOY. During early winter, relative abundance was highest at mid-range depths (20-30 m) but shifted toward greater depths (> 35 m) during later winter months (Figure 3.5). Striped bass were likely to occur over a broader range of depths during spring, but were predicted to have the highest abundance at depths between 25 and 30 m. The optimal model had a 0.05 error rate compared to the maximum (maximum=15; RMSE 0.84 ± 0.07) with an average error <0.01 (average error 0.003 ± 0.022) calculated by k-fold cv score. There was no residual spatial or temporal autocorrelation patterns apparent in ACF, PACF, of semi-variogram plots (Appendix, Figure A.3; A.4).

Individual and environmental drivers of residency

Inclusion of the first-order lagged weekly occurrence markedly improved residual temporal autocorrelation in all individual residency models for both species (Appendix, Figure A.5; A.6). Although addition of second and third order correlation terms increased the explained deviance, these terms added excess complexity and did not considerably improve ACF and PACF-visualized autocorrelation. Analysis thus proceeded with the use of a first-order autocorrelation structure, or 1-day state-dependence residency lag only.

The weekly residency models for Atlantic sturgeon and striped bass showed that SST and week-of-year were significant predictors of the number of days individuals were present in the array (Table 3.3). However, unlike predictive habitat models, CHL-A concentration was not a significant predictor of Atlantic sturgeon occupancy at the $\alpha = 0.05$ level. The residency model for Atlantic sturgeon showed that the individual random effect was important and that response differed between Chesapeake Bay vs. South Carolina Rivers, Chesapeake Bay vs. Virginia Rivers, and Coastal Delaware vs. Virginia River tagging regions (Table 3.3: Wald test, $p < 0.05$). For striped bass, the effect of CHL-A concentration on residency was significant; however, the random effect of transmitter was not significant. Pairwise comparison between tagging regions revealed differences in response between the Delaware River vs. Coastal Massachusetts and Delaware River vs. Hudson River origins (Table 3.3: Wald test, $p < 0.05$).

Partial effects of environmental and temporal variables in species residency GAMMs were largely consistent with the responses observed in relative abundance

modeling, but revealed variation in how these factors affected the amount of time individuals spent in the area. Additionally, contrasts between species were apparent. Atlantic sturgeon had a bimodal response to SST in which individuals were more likely to occupy the region when weekly, array-wide surface temperatures were around 10°C or 20°C (Figure 3.6). Temperatures between and outside these general ranges had a negative effect on sturgeon residency. Week-of-year was the most significant term in the model and showed that Atlantic sturgeon occupancy was highest during spring and autumn, with peaks in the number of days present around week 20 (mid-May) and week 45 (mid-November), respectively. In contrast to Atlantic sturgeon, partial effects showed that temperatures <15°C were associated with higher striped bass residency while temperatures higher than this threshold negatively affected residency duration (Figure 3.7). Similar to the GAMM abundance model, striped bass were likely to occur for more days per week during winter and spring months and were unlikely to reside in the area during summer. Though CHL-A observations were skewed, striped bass occupancy was highest when concentrations were either just above 0 mg m^{-3} or very high between 10-20 mg m^{-3}.

Population-level differences in residency response

HGAM-predicted residency revealed that Atlantic sturgeon responded differently to SST and week-of-year depending on their tagging origin. For sturgeon tagged in the Chesapeake Bay, Santee River, and Virginia Rivers, longer residency was most likely when SST was between 15-20°C (Figure 3.8). The group tagged off the Atlantic coast of Delaware differed in that individual residency was more likely at

lower surface temperatures between 10-15°C. The highest predicted increases in residency in response to SST occurred for the Chesapeake Bay and South Carolina River groups. Individuals tagged in coastal Delaware and Virginia Rivers did not show the same magnitude of response to SST and were predicted to reside in the array for less time. There were also group-level differences in timing of arrival and amount of seasonal residency for Atlantic sturgeon in response to week-of-year. The week-of-year hierarchical model showed that degree of residency was fairly similar between spring and fall for sturgeon tagged in the South Carolina and Virginia Rivers (Figure 3.9). In contrast, individuals tagged on the Atlantic Coast of Delaware and in the Chesapeake Bay were more likely to reside longer in the area during autumn compared to spring. Sturgeon tagged off Delaware were predicted to arrive slightly earlier in the MD WEA array over both migration seasons compared to relatively later arrivals and peaks in residency for the Chesapeake Bay and Virginia tagging regions.

Group-level differences occurred in how striped bass responded to SST and week-of-year, but variation in response to CHL-A concentration was less apparent. Residency predictions were highest when SST was < 15°C, with striped bass tagged in the Delaware and Potomac Rivers showing peaks in the number of days detected at 10°C (Figure 3.10). Individuals tagged in coastal Massachusetts and the Kennebec River had a slightly flatter response to SST and were predicted to reside for less time over a broader range of temperatures (5-10°C) compared to the other groups. All tagging regions showed a similar pattern of lower residency in the spring and higher residency in the winter, but individuals tagged in the Hudson River were

predicted to occupy the region for the greatest amount of time in both seasons (Figure 3.11). The peak in spring residency also appeared to occur slightly earlier in the spring for Hudson fish compared to other groups. Group-level heterogeneity was not obvious in the response of striped bass to chlorophyll-a concentration (Figure 3.12).

Discussion

The three models all showed that readily available habitat variables provided seasonal predictions across the MD WEA and adjacent regions for two important species. The gradient acoustic telemetry survey design allowed species occurrence to be efficiently matched to key environmental variables of depth, SST, Δ SST, and CHL-A and supported robust model fitting with moderately precise and ecologically feasible predictions. Though receiver resources with which to measure and assess presence of acoustically-tagged fish were limited, the gradient design allowed species occurrence to be modeled throughout an intercept region of a multi-species migration corridor. I was able to make inferences more robust through weighted adjustment of detection range. Receiver detection range dynamics should be understood because detectability patterns can lead to false inferences regarding species biology (Payne et al. 2010). For instance, high levels of ambient noise caused by wind events can interfere with acoustic tag detection rates (Secor et al. 2019b) as can seasonal changes in stratification (Secor et al. 2019a). Including detection range weighting significantly reduced temporal autocorrelation, which suggests that raw counts of individuals were influenced by underlying patterns in tag detectability.

Spatiotemporal drivers of relative abundance

Dynamic habitat modeling reinforced previous results that striped bass and Atlantic sturgeon incidence varies according to shelf environmental gradients. Notably, predictive models confirmed seasonal shifts in depth preference; both species occurred in inner/mid-shelf depths - those associated with the MD WEA - but sturgeon were more likely to utilize shallower areas during the spring and striped bass were more abundant at deeper waters in late winter. The protracted winter presence of striped bass near Maryland's outer shelf is a relatively new finding (see Chapter 2), but similar seasonal variation in Atlantic sturgeon distribution has been observed previously in the MAB (Stein et al. 2004; Laney et al. 2007; Erickson et al. 2011; Breece et al. 2017). These spatiotemporal shifts in shelf incidence may indicate differential behaviors or habitat requirements between the northern and southern migrations of these two species. The relative abundance of Atlantic sturgeon and striped bass could have been further influenced by oceanographic features such as bottom temperature, frontal dynamics, or wind conditions that were not incorporated in predictive modeling due to concurvity or data resolution issues. Although we cannot say with absolute certainty which factors drive species migrations and incidence, the interaction between depth and DOY served as a relatively strong predictor of species abundance, making these variables most relevant from a management perspective. While the strength of DOY and depth as predictors of abundance may be indicative of broader migration cues and characteristics that correlate with seasonal and spatial variables, I maintain that these models provide

valuable information for stakeholders that can be further improved through future research.

The importance of distinct and contrasting magnitudes of SST change for each focal species likely relate to differences in shelf distribution and migration behavior. Atlantic sturgeon were more likely to occur when SST had either decreased moderately or increased greatly over the previous 4 days. In comparison, striped bass incidence was highest when SST had either decreased or remained relatively constant over the previous 17 days. The significance of shorter time lags may indicate faster transit rates for Atlantic sturgeon, where they are responding to more subtle changes in temperature. A shorter temperature cue could also indicate a more local response to temperature. Results may therefore suggest that Atlantic sturgeon are located closer to the MD WEA, in nearby coastal regions, when they initiate movements, while striped bass might be located farther away when they respond to migration cues. Still, a greater lag in temperature change response could also reflect slower transit of striped bass through the region. Though SST is likely to be variable along longitudinal gradients during seasons of Atlantic sturgeon and striped bass shelf incidence (Yoder et al. 2002; Kohut et al. 2004; He et al. 2010), lagged SST likely represents a broadly-applicable proxy that could apply to other regions within the MAB.

Although consistently less significant in the model selection process, CHL-A concentration was found to further modify the relative abundance of striped bass and sturgeon in shelf waters. Atlantic sturgeon were associated with two relatively low CHL-A concentration peaks while striped bass abundance was highest when there were either very low or high CHL-A concentrations. CHL-A values are typically less

than 3 mg m^{-3} in the MAB, which was the case in this study, but much higher concentrations can occur during winter and spring blooms, some of which develop as early as January (O'Reilly and Zetlin 1998; Xu et al. 2011). The first prolonged occurrence of striped bass, recorded during winter 2017, was associated with one such high-chlorophyll event that reached 10-20 mg m^{-3}. Relationships between CHL-A concentration and species abundance may thus ultimately be correlative. However, chlorophyll concentrations are often related to shelf productivity and could reflect conditions where forage fish such as Atlantic menhaden are more abundant and available to striped bass (Friedland et al. 1996; Frank et al 2006; Annis et al. 2011; Friedland et al. 2012). Aside from the winter 2017 anomaly, most CHL-A concentrations were less than 5 mg m^{-3} throughout the array, with a general pattern of higher concentrations inshore. Increased chlorophyll concentration nearshore is likely related to upwelling dynamics as well as outflows of nutrients from terrestrial sources (Yoder et al. 2001; Shofield et al. 2008; Xu et al. 2011). Atlantic sturgeon near the Delaware Bay have been found to prefer specific reflectance wavelengths that are associated with terrigenous outputs, so sturgeon may have had higher incidence at specific CHL-A concentrations near 2 and 5 mg m^{-3} because of river plume sources (Oliver et al. 2013; Breece et al. 2016). The dual peak in CHL-A association might also simply be coincident with known seasonal migration behaviors causing increased sturgeon incidence during fall and spring (Breece et al. 2018). It should be also noted that remotely-sensed CHL-A values can be biased representations because they are only surface measures. Chlorophyll dynamics are obscured by turbidity in coastal regions and are often more complex beneath the mixed layer (Chen et al. 2013; Xu et

al. 2013). Thus, only correlative support should be inferred for relationships between surface chlorophyll and species distribution; more definitive links would require careful foodweb analysis of the region (e.g. Woodland and Secor 2013).

Environmental and individual determinants of residency

The combination of environmental predictors with individual characteristics further provided valuable baseline information on the drivers of species residency within the region. The models presented here will inform management decisions regarding how to avoid harmful interactions with species of concern. My results also provide context for how populations of striped bass and sturgeon may be differentially affected by regional wind energy development.

Model predictions showed that timing of environmental changes and shelf gradients drove patterns of species residency in the study array. Generally, Atlantic sturgeon occupancy was highest during autumn and spring when SSTs were between 10-20°C. This range is consistent with past telemetry work in the MAB, which found that Atlantic sturgeon occurred most frequently between 10-20°C with a peak in incidence around 18°C SST (Breece et al. 2017). The present study identified a similar peak, near 18°C, that resulted in the highest weekly occupancy in the region. The temperature ranges associated with increased residency are supported by previous bioenergetic studies in which sturgeon metabolic rates (albeit those of juveniles < 1 m total length) increased with temperature but leveled off at warmer extremes of 24-28°C (Niklitschek and Secor 2009; 2010). Other work has suggested that temperature is key in structuring Atlantic sturgeon movement behavior. In the

Delaware Bay, adult Atlantic sturgeon are known to transition from resident to movement behaviors when water temperatures decrease below 18-19°C (Breece et al. 2018). SSTs between 15-20°C may thus provide particularly favorable conditions for Atlantic sturgeon that result in slower migration along the MAB shelf.

Evidence showed that sturgeon tagged in the Atlantic Ocean off Delaware were more likely to reside during slightly cooler SSTs between 10-20°C in comparison to those tagged in more southern regions. This apparent difference could indicate that fish tagged in these regions are more tolerant of a range of conditions and that they are likely to reside in habitats more widely spread across the shelf. However, coastal Delaware sturgeon had the earliest peaks in residency during both seasons, so it may be difficult to infer whether individuals have broader temperature tolerance or simply coincidentally occur at cooler temperatures in the spring and warmer temperatures in the fall due to their divergent migration timing. Additionally, I found that Atlantic sturgeon tagged in South Carolina and Virginia Rivers were likely to have the same magnitude of residency over both migration seasons while those tagged in coastal waters and the broader Chesapeake Bay were more likely to spend more days in the array during autumn compared to spring. Although true genetic origin was not available in this study, sturgeon tagged in the South Carolina Rivers (Edisto, Pee Dee, and Santee Rivers) and Virginia Rivers (York, James, Pamunkey Rivers) likely represent a larger proportion of sturgeon that originated from these spawning tributaries in comparison to other groups, which are known mixed-population aggregations including the dominant Hudson River population (Dunton et al. 2012; Wirgin et al. 2015a; b). Longer fall residency times for

Chesapeake and Atlantic coast fish may therefore reflect that these groups comprise individuals from the Hudson River population, which is known to aggregate in coastal habitats near the Chesapeake and Delaware estuary mouths (Erikson et al. 2011). In contrast, the shorter predicted residency for Virginia and South Carolina River fish suggests that these tagging groups may be using winter habitat farther south. However, recent findings indicate that coastal stocks of Atlantic sturgeon are made up of a higher number of contributing populations than previously thought and that straying within non-natal rivers can occur (ASMFC 2017). Thus, tagging-origin differences should be interpreted with caution.

Striped bass differed from Atlantic sturgeon in that cooler SSTs predicted increased residency. Striped bass were also more likely to be detected for multiple days during winter months compared to spring. This finding was consistent with previous results showing faster migrations for striped bass during spring with increased likelihood of residency during winter (Kneebone et al. 2014; Callihan et al. 2015; see Chapter 2). Peaks in striped bass residency corresponded to SSTs near 10°C, which is considerably lower than thermal niches reported for striped bass in landlocked environments, which are thought to range between 18 to 25°C (Coutant 1985) with a hypothesized fundamental niche between 19-23°C (Coutant 1990). However, striped bass are known to acclimate to a remarkably wide range of temperatures; the species may tolerate temperatures up to 30°C to avoid hypoxic conditions (Jackson and Hightower 2001; Thomson et al. 2010; Kraus et al. 2015) and remain active as low as 1.0°C (Clark 1968; Tagatz 1961). Indeed, more recent studies have confirmed that the thermal niche for striped bass includes temperatures

as low as 13 °C (Bettoli 2005; Nelson et al. 2010). These lower temperatures, which are more similar to the conditions that supported striped bass residence in my results, better align with temperatures thought to provide "optimal" growth for striped bass (14–15°C; Hartman and Brandt, 1995). While I cannot state whether temperatures near 10°C truly support increased physiological performance in striped bass without further mechanistic investigation, these temperatures are likely more favorable for striped bass than the comparatively cooler temperatures that occur in nearshore regions during winter and early spring months (see Chapter 2). However, more in-depth research will be needed to evaluate how outer shelf winter conditions, which may include oceanographic fronts and eddy dynamics along with favorable temperatures, influence the habitat selection and subsequent physiological outcomes in striped bass.

Striped bass showed only modest differences in tagging-origin groups in their residency patterns. Residency for striped bass tagged in Chesapeake and Delaware estuaries peaked at 10°C temperatures, while fish tagged in regions North of Delaware were likely to reside for a longer period when SSTs were between 0-10°C. These northern groups (tagged in Maine and Massachusetts) were also the most likely to inhabit the region throughout winter and spring. Broader and lower temperature preference for these groups may therefore reflect their northern origin, and acclimatization and/or genetic selection to colder temperatures. Striped bass tagged in the Hudson River tended to arriver earlier during spring and reside longer than other tagged groups. This difference supports a hypothesis proposed by Waldman et al. (2012) that Hudson River striped bass over-winter in waters farther north than Cape

Hatteras. The authors suggested that this behavior would represent a geographic trade-off: although warmer, metabolically preferable waters are located near North Carolina in winter, shorter migration would be energetically less taxing. Though I was able to detect differences in striped bass residency between tagging regions, fish tagged in Massachusetts are likely comprised of multiple spawning stocks (Kneebone et al. 2014) and individuals have been known to enter non-natal estuaries (Grothues et al. 2009). Similar to the sturgeon tagging origin analysis, my findings should thus be considered preliminary and warranting further investigation with regard to genetic assignments to populations of origin.

Management implications and opportunities for future research

The dynamic habitat models fitted to relative abundance and residency relied on relatively few predictor variables, but these can be readily obtained from satellites and other observing platforms. While other dynamic oceanographic features likely influence the seasonal distribution of fish species in the region, many variables were not available at the data resolution necessary for daily, fine-scale analysis. Dynamic habitat models for marine fish, turtles, birds, and mammals have found that mesoscale oceanographic features such as eddies, thermal fronts, upwelling zones, and wind-driven mixing play key roles in structuring species distribution in pelagic habitats (Bigelow et al. 1999; Nel et al. 2001; Benson et al. 2001; Kai and Marsac 2010; Hobday and Hartog 2014; Hazen et al. 2017). However, cloud cover is a common limitation to satellite observations of such dynamics in the nearshore MAB. To better understand the biological drivers of species behavior, future studies could incorporate

modeled oceanographic dynamics from products like the Finite-Volume Community Ocean Model (FVCOM: Chen et al. 2003) or the Regional Ocean Modeling System (ROMS; www.myroms.org), which may enable more robust inferences surrounding species behavior and movement decisions (e.g. Zemeckis et al. 2017; Breece et al. 2018; Secor et al. 2019b). Future modeling might benefit from the use of variables such a photosynthetically-active radiation (PAR), sea surface temperature anomaly, or blended ocean color products as drivers of abundance or incidence in place of DOY, lagged SST, or CHL-A concentration, respectively. These variables could provide more interpretable or biologically-relevant predictors for the migratory behavior of the multiple species transiting through the MAB flyway. Mechanistic models, which couple animal physiology (e.g., thermal performance) with environmental associations (Niklitschek and Secor 2005; Kearney and Porter 2009; Payne et al. 2018), would also help elucidate potential biological or physiological drivers of shelf habitat selection. Emerging acoustic telemetry technologies such as depth-transponding tags, accelerometers, or condition-sensing transponders could provide useful methods for elucidating dynamics such as water column depth preference or physiological drivers of species movement along the shelf.

Despite the potential limitations of presented biological inferences, the relative abundance models developed by this study performed well, with 80% and 60% deviance explained (for Atlantic sturgeon striped bass, respectively), and were thus able to predict species presence using only a few, readily-accessible, environmental variables. The predictors used in this study can thus be easily attained and used by developers to decide when potentially disruptive activities should take

place or be avoided. Similar predictive models have been used in the past to inform near real-time advisories or area closures that help limit harmful interactions with species of concern (Hobday et al. 2010; Laist et al. 2014; Dunn et al. 2016).

Model results can be used to help identify particular temperatures or weekly periods in which species might be more vulnerable to regional impacts due to anthropogenic activities. From a wind energy construction standpoint, developers can expect that summer months will provide the most favorable window for wind turbine installation for the two focal species, since striped bass and Atlantic sturgeon were reliably absent during these time frames. Individual-based modeling also allowed me to assess the factors that influence how long species seasonally occupy the MD WEA. Although I was able to discern group-level heterogeneity in response between tagging regions, patterns of residency were relatively similar overall. These results suggest that behavioral differences between tagging groups are limited and that coastal stocks of Atlantic sturgeon and striped bass can be treated similarly at the level of concern to wind energy developers. Here, interactions with all tagging origin groups examined could be broadly avoided by limiting construction activities between November and May for striped bass and during periods March-June and November-December for Atlantic sturgeon. Reduction in potential construction or vessel traffic disruptions during these time periods would similarly avoid interactions with other critical large whale species, including fin, humpback, minke, and North Atlantic right whales, which are primarily detected from November to April in the Maryland shelf region (Bailey et al. 2018). However, hierarchical modeling of individual characteristics such as genetic origin, sex, or size could reveal important differences in regional

occupancy of striped bass and Atlantic sturgeon and these factors should be considered in future studies.

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Tables

Table 3.1. Summary of intended purpose and modeling approach for each research question. See Methods for additional explanation. GAMM=Generalized Additive Mixed Model; HGAM=Hierarchical Additive Mixed Model.

Category	*Objective*	*Modeling approach*	*Response variable*	*Level of organization*	*Autocorrelation compensation*	*Random effects*
Relative abundance	Predict fine-scale relative abundance of test species	GAMM	Number of individuals per receiver	Temporal: Daily Spatial: Receiver-based	Range test offset	Receiver site and Year of study
Individual weekly residence	Determine predictors of individual residence	GAMM	Number of days per week	Temporal: Weekly Spatial: Array-wide	Lagged residency response	Individual ID
	Evaluate residence response by population (tagging origin)	HGAM submodel	Number of days per week	Temporal: Weekly Spatial: Array-wide	Lagged residency response	Tagging origin

Table 3.2. Summary of GAMM model equation terms, degrees of freedom (df), Akaike information criterion (AIC), and percent deviance explained for the top ten predictive habitat models for each species, ordered by AIC score. Considered predictors are chlorophyll-a concentration (CHL-A), magnitude of SST change (SST Δ1-13), day-of-year (DOY), and depth. Model term "s" represents singular smooth terms (single factors) and "t2" represents tensor-product smooth interactions (interaction between factors with different scales). Selected models are at the top of the table for each species.

Model terms	*df*	*AIC*	*Deviance explained*
Atlantic Sturgeon			
s(CHL-A) + s(SST Δ4) + t2(DOY, Depth)	51.99133	5042.376	79.9%
s(CHL-A) + s(SST Δ2) + t2(DOY, Depth)	53.02093	5043.901	79.9%
s(CHL-A) + s(SST Δ3) + t2(DOY, Depth)	52.58188	5044.783	80%
s(CHL-A) + s(SST Δ23) + t2(DOY, Depth)	53.71414	5045.779	79.7%
s(SST Δ4) + t2(DOY ,Depth)	45.59794	5047.142	79.5%
s(SST Δ2) + t2(DOY, Depth)	46.97376	5047.626	79.4%
s(CHL-A) + s(SST Δ9) + t2(DOY, Depth)	52.24633	5047.696	79.5%
s(SST Δ3) + t2(DOY, Depth)	46.65425	5049.766	79.5%
s(CHL-A) + s(SST Δ5) + t2(DOY, Depth)	50.25464	5050.407	79.7%
s(CHL-A) + s(SST Δ22) + t2(DOY, Depth)	52.45791	5050.455	79.5%
Striped Bass			
s(CHL-A) + s(SST Δ17) + t2(DOY, Depth)	57.19528	7090.493	60.1%
s(CHL-A) + s(SST Δ16) + t2(DOY, Depth)	56.85801	7103.559	60.1%
s(CHL-A) + s(SST Δ19) + t2(DOY, Depth)	57.85631	7112.665	59.6%
s(SST Δ17) + t2(DOY, Depth)	52.41223	7116.058	59.9%
s(CHL-A) + s(SST Δ18) + t2(DOY, Depth)	57.08371	7123.809	59.5%
s(SST Δ16) + t2(DOY, Depth)	52.65560	7125.717	59.9%
s(SST Δ19) + t2(DOY, Depth)	52.26835	7141.836	59.4%
s(SST Δ18) + t2(DOY, Depth)	52.31685	7147.398	59.3%
s(CHL-A) + s(SST Δ20) + t2(DOY, Depth)	58.17577	7159.898	58.6%
s(CHL-A) + s(SST Δ15) + t2(DOY, Depth)	56.28915	7161.697	58.9%

Table 3.3. Parameter and pairwise factor comparison significance for weekly species residency GAMMs. Significance of model parameters and pairwise tagging region factors (Origin) are indicated by asterisks (<0.001= ***; 0.001-0.009 =**; 0.01-0.009=*; 0.05-0.1=.). For Atlantic sturgeon, tagging regions are CB = Chesapeake Bay; SC = South Carolina Rivers; DE Coast = Atlantic Coast of Delaware; VA = Virginia Rivers. Striped bass tagging regions are: Hudson = Hudson River, New York; Potomac = Potomac River, Maryland; MA = Coastal Massachusetts; Kennebec = Kennebec River, Maine.

Species	*Term*	*p-value*	*df*	*AIC*	*Deviance explained*
Atlantic Sturgeon					
	s(SST)	0.017 *	85.20	7453.49	68.6%
	s(Week)	<0.001 ***			
	s(CHL-A)	0.112			
	s(Lag 1 Residency)	<0.001 ***			
	s(Transmitter)	0.012 *			
	Origin: CB with SC	0.039 *			
	Origin: DE Coast with SC	0.058 .			
	Origin: CB with VA	0.033 *			
	Origin: DE Coast with VA	0.028 *			
	Origin: DE Coast with CB	0.503			
	Origin: SC with VA	0.542			
Striped Bass					
	s(SST)	<0.001 ***	25.83	9899.17	56.2%
	s(Week)	<0.001 ***			
	s(CHL-A)	<0.001 ***			
	s(Lag 1 Residency)	<0.001 ***			
	s(Transmitter)	0.593			
	Origin: Hudson with Potomac	0.200			
	Origin: Hudson with Kennebec	0.417			
	Origin: MA with Potomac	0.255			
	Origin: Hudson with MA	0.674			
	Origin: Kennebec with Potomac	0.789			
	Origin: DE River with Potomac	0.967			
	Origin: DE River with Kennebec	0.767			
	Origin: Kennebec with MA	0.507			
	Origin: DE River with MA	0.025 *			
	Origin: DE River with Hudson	0.025 *			

Figures

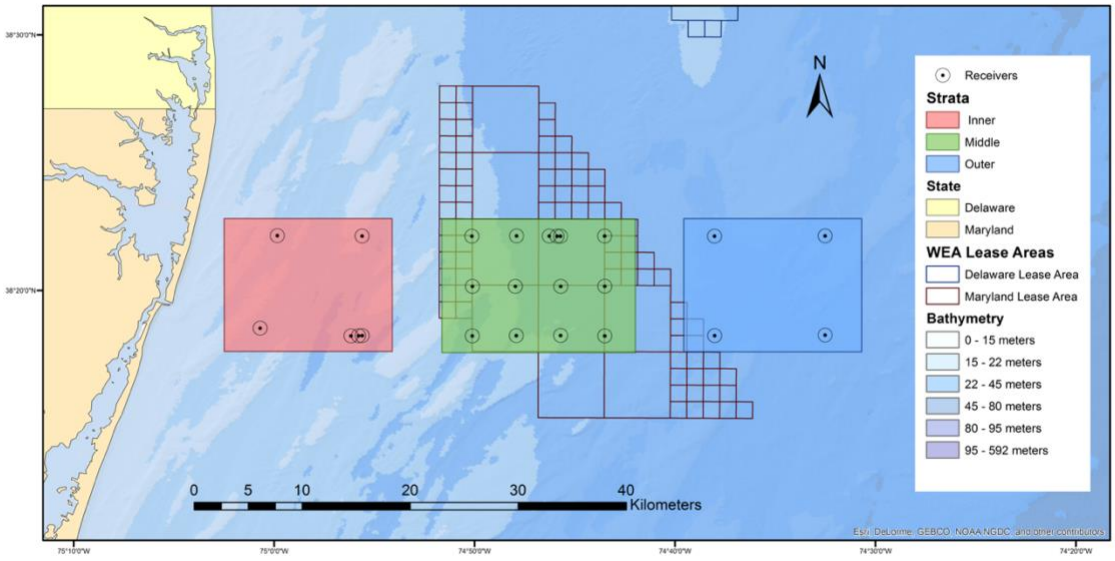

Figure 3.1. Map of study region off the coast of Maryland including acoustic receiver array design and bathymetry features. Circles surrounding receivers represent the maximum expected 1000 m detection radius and range test sites are shown within the Inner and Middle Strata as overlapping circles of presumed detection range.

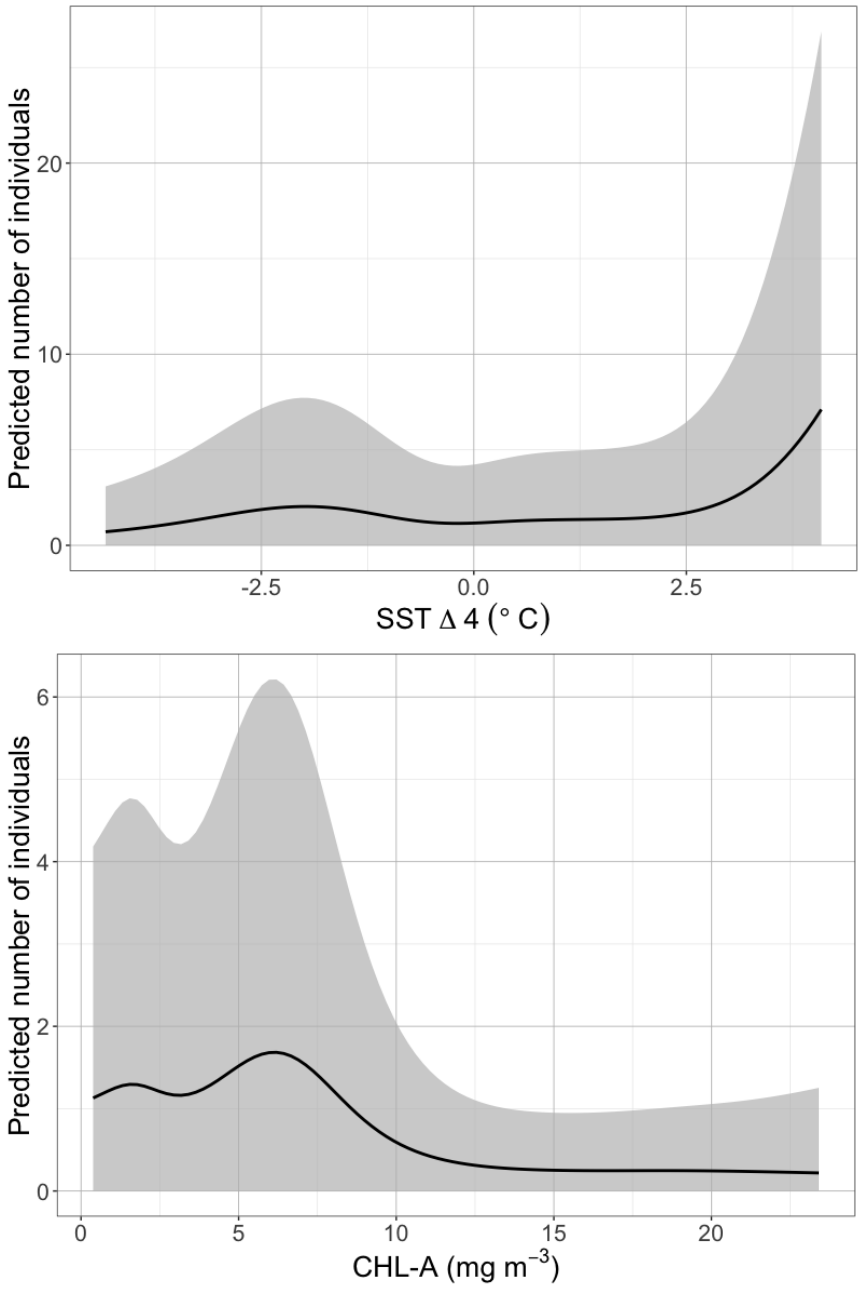

Figure 3.2 . GAMM Summed effects of the magnitude of sea surface temperature change over the previous 4 days (SST Δ4; top) and chlorophyll-a concentration (CHL-A; bottom) on the relative abundance of Atlantic sturgeon. Shading represents ± 2 standard error. Both predictions are made on day-of-year =300 and depth=15 m to represent conditions when sturgeon are expected to occur. Mean SST Δ4 and CHL-A were set as the conditions in each corresponding prediction. Random effects were excluded to allow for interpretability across all sites and years.

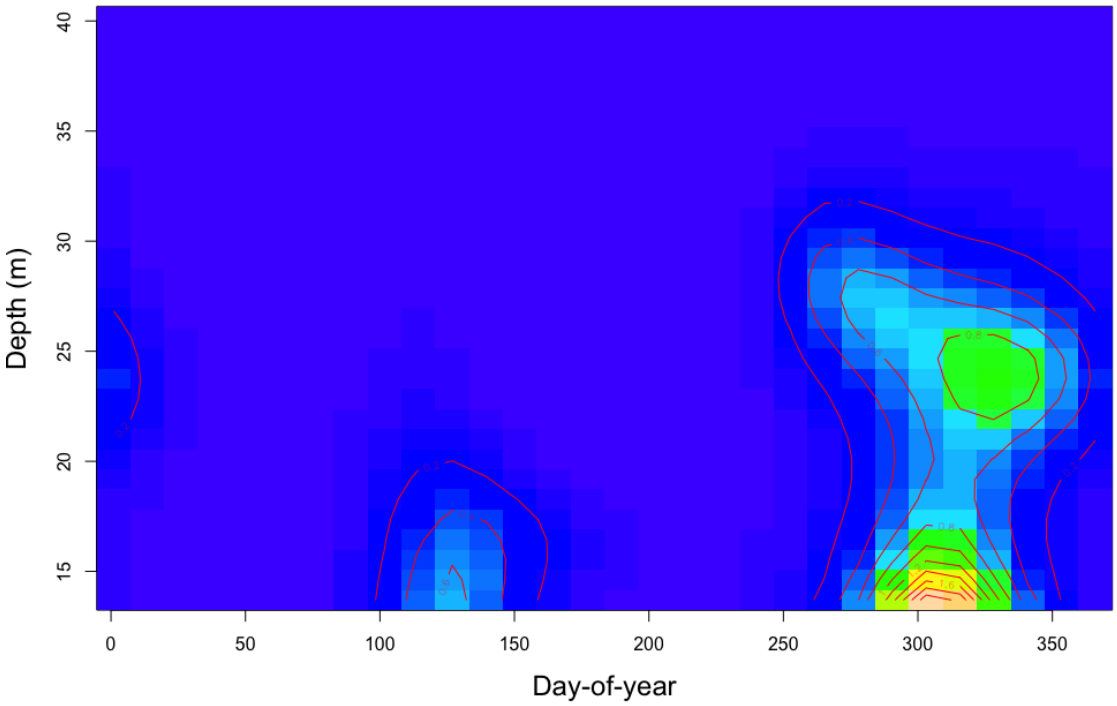

Figure 3.3. GAMM response function for the interaction between day-of-year and depth from the best model of Atlantic sturgeon relative abundance. Visualizations are on the response scale and warmer colors indicate a higher predicted number of individuals.

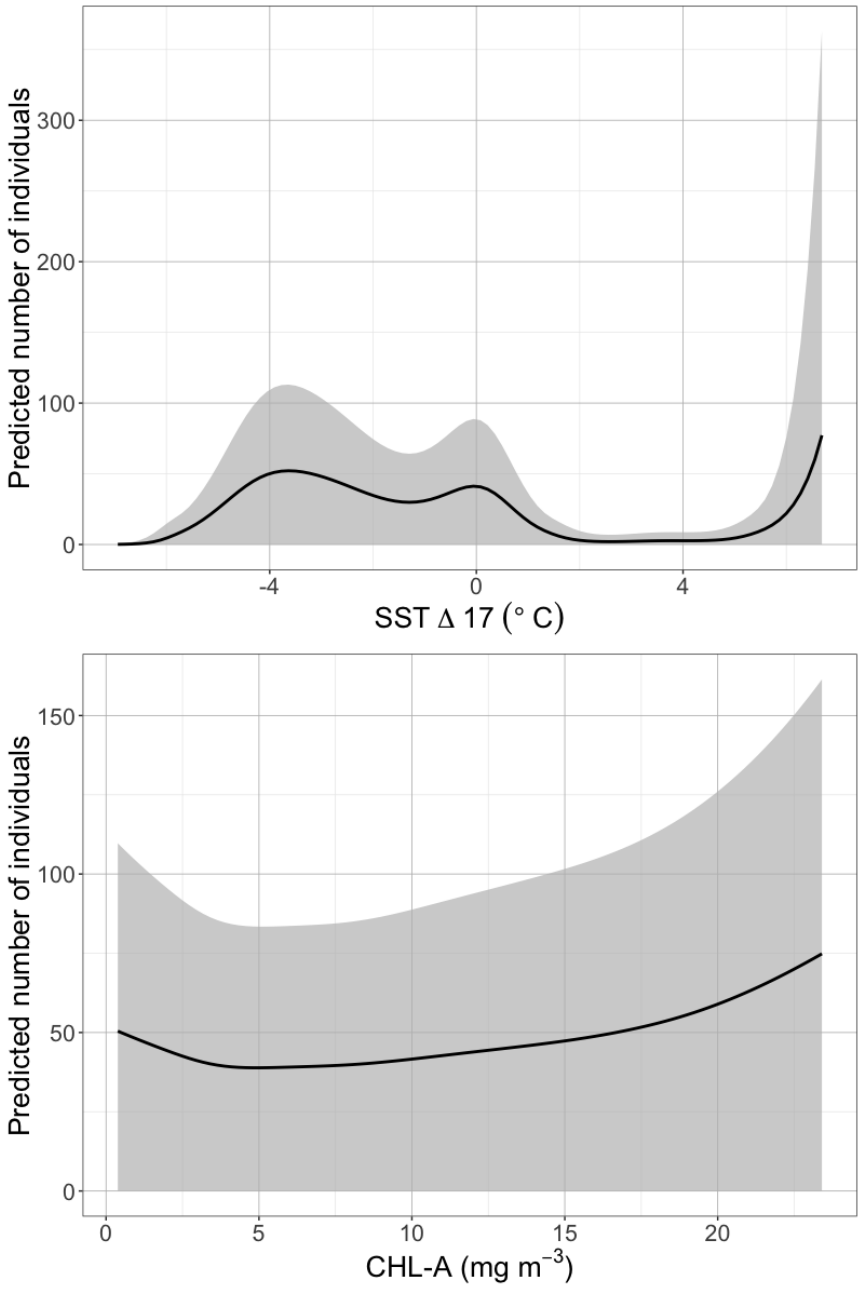

Figure 3.4. GAMM Summed effects of magnitude of sea surface temperature change over the previous 17 days (SST Δ17; top) and chlorophyll-a concentration (CHL-A; bottom) on the relative abundance of striped bass. Shading represents ± 2 standard error. Both predictions are made on day-of-year =350 and depth=25 m to represent conditions when striped bass are expected to occur. Mean SST Δ17 and CHL-A were set as the conditions in each corresponding prediction. Random effects were excluded to allow for interpretability across all sites and years.

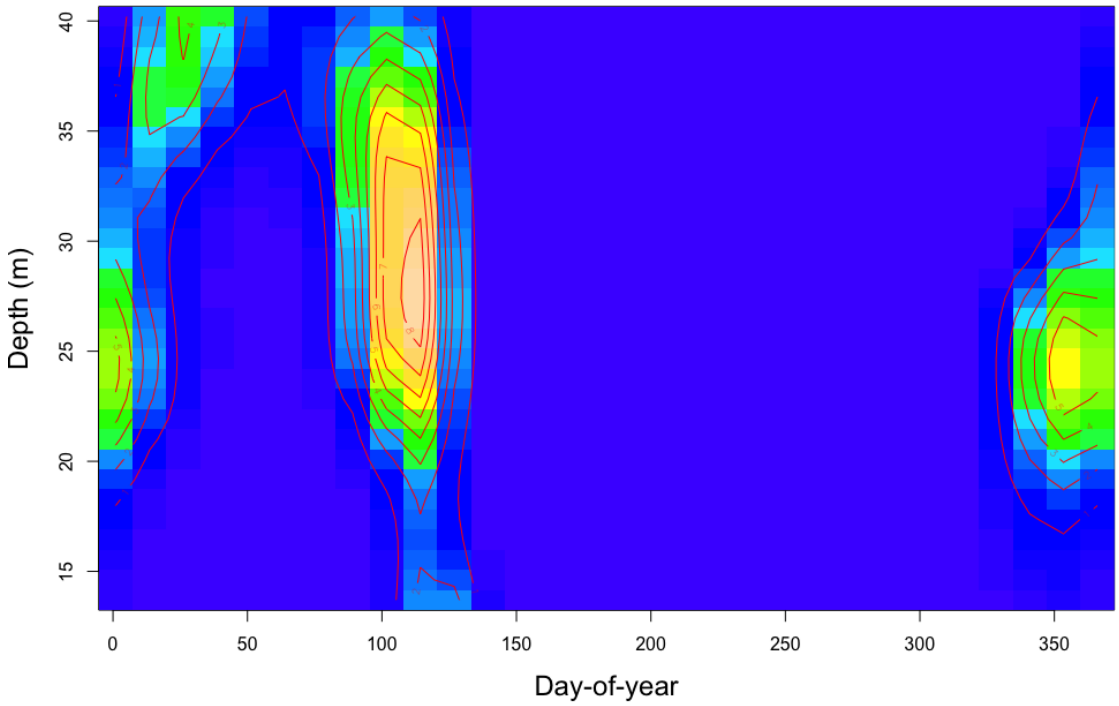

Figure 3.5. GAMM response function for the interaction between day-of-year and depth from the best model of striped bass relative abundance. Visualizations are on the response scale and warmer colors indicate a higher predicted number of individuals.

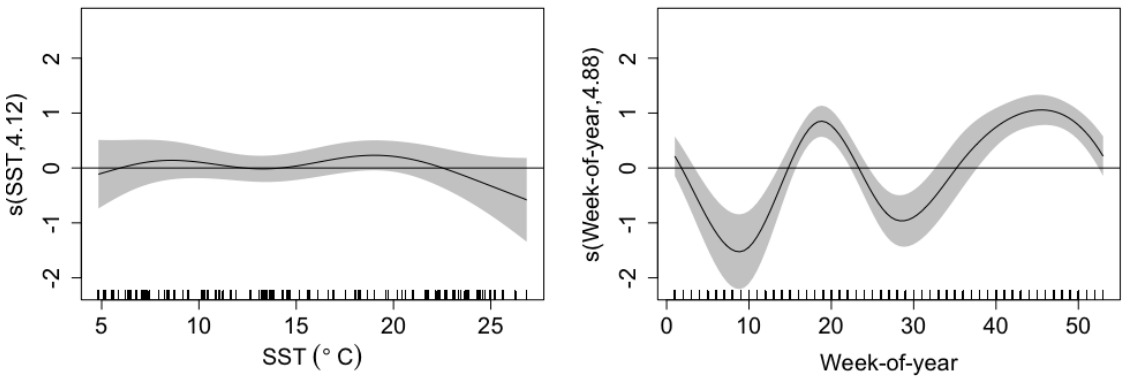

Figure 3.6. Atlantic sturgeon: GAMM partial effects for sea surface temperature (SST, left), week-of-year (right). Chlorophyll-a concentration not plotted due to lack of significance. Rugs along the x-axis represent the distribution of observations.

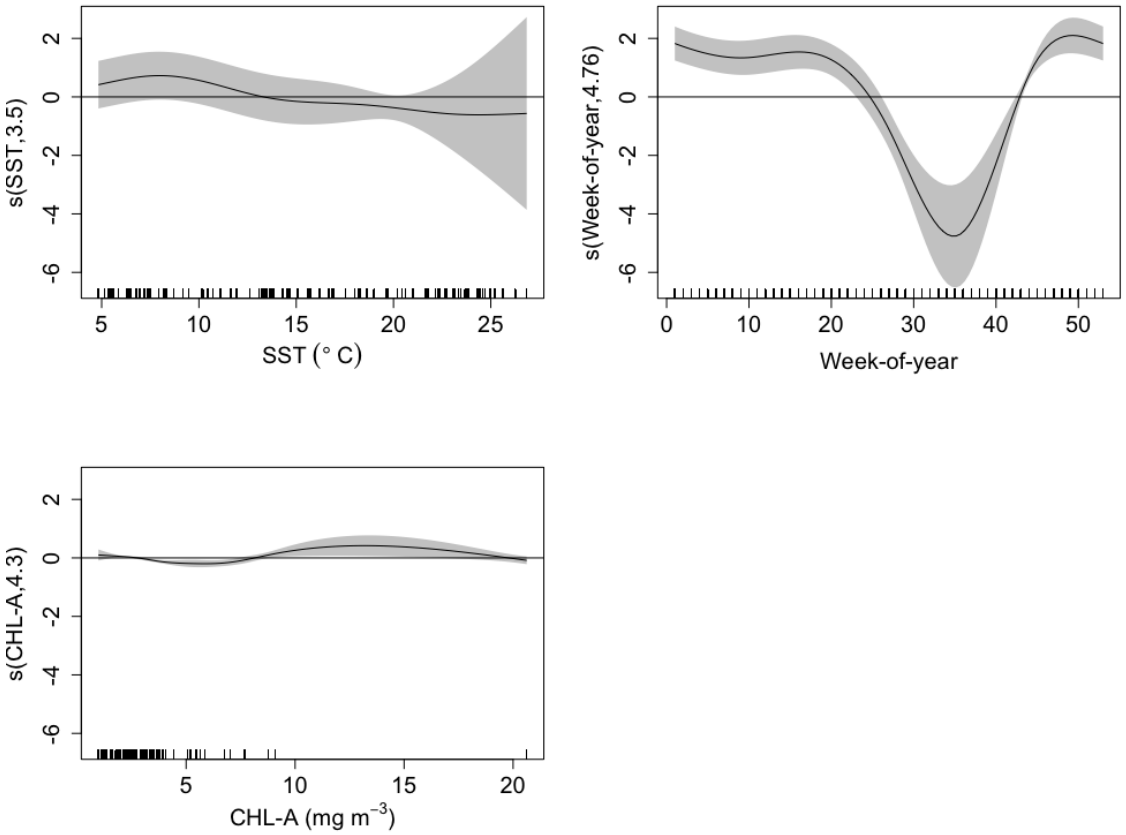

Figure 3.7. Striped bass: GAMM partial effects for sea surface temperature (SST, top left), week-of-year (top right), and chlorophyll-a concentration (CHL-A, bottom left). Rugs along the x-axis represent the distribution of observations.

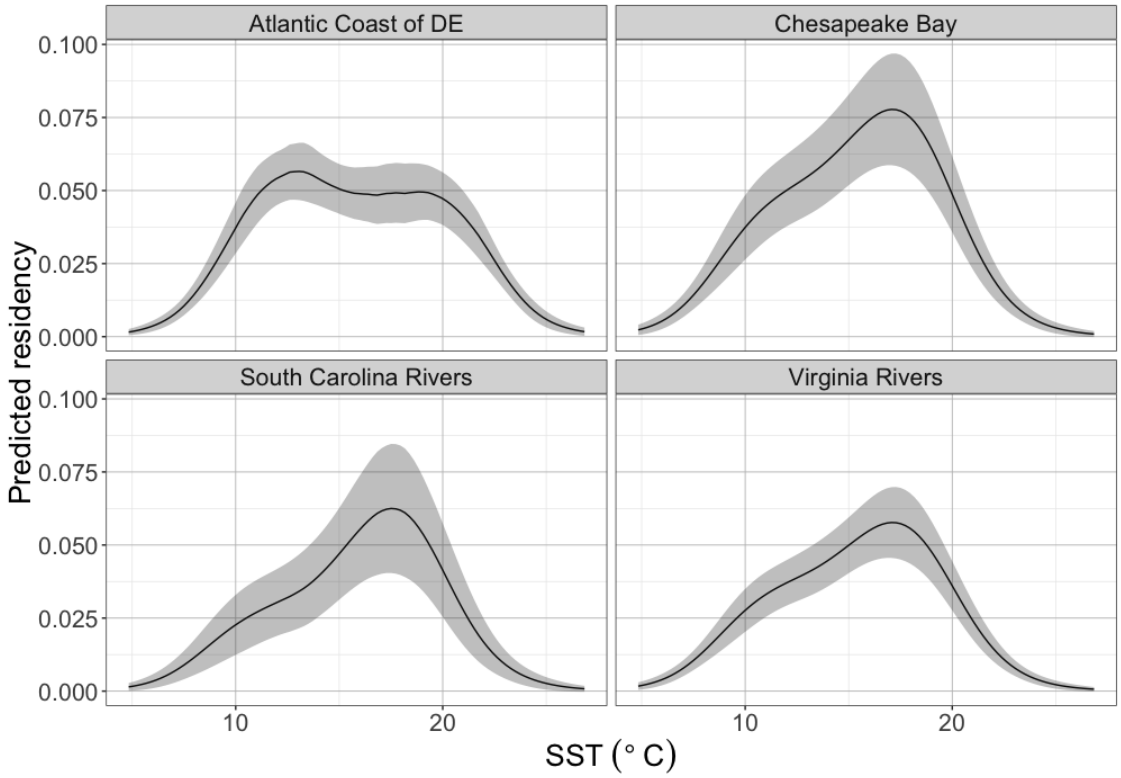

Figure 3.8. Predicted residency function (days per week ± 2 se) of Atlantic sturgeon for each tagging region based on the sea surface temperature (SST) across the MD WEA.

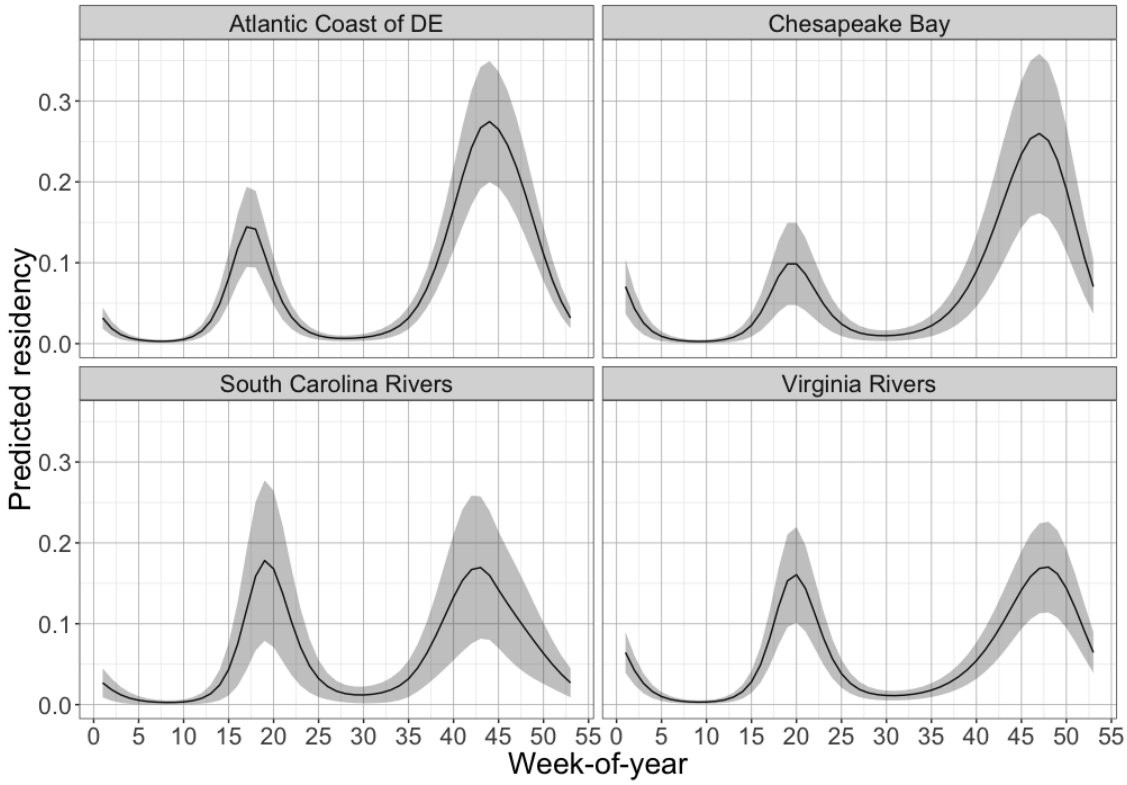

Figure 3.9. Predicted residency function (days per week ± 2 se) of Atlantic sturgeon in the MD WEA array for each tagging region based on week-of-year.

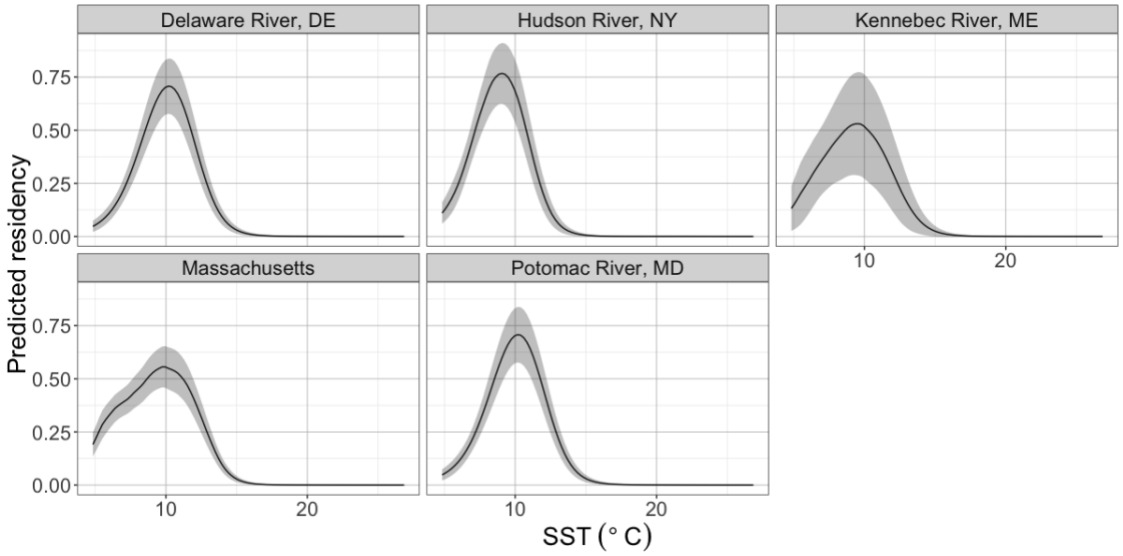

Figure 3.10. Predicted residency function (days per week ± 2 se) of striped bass for each tagging region based on the sea surface temperature (SST) across the MD WEA.

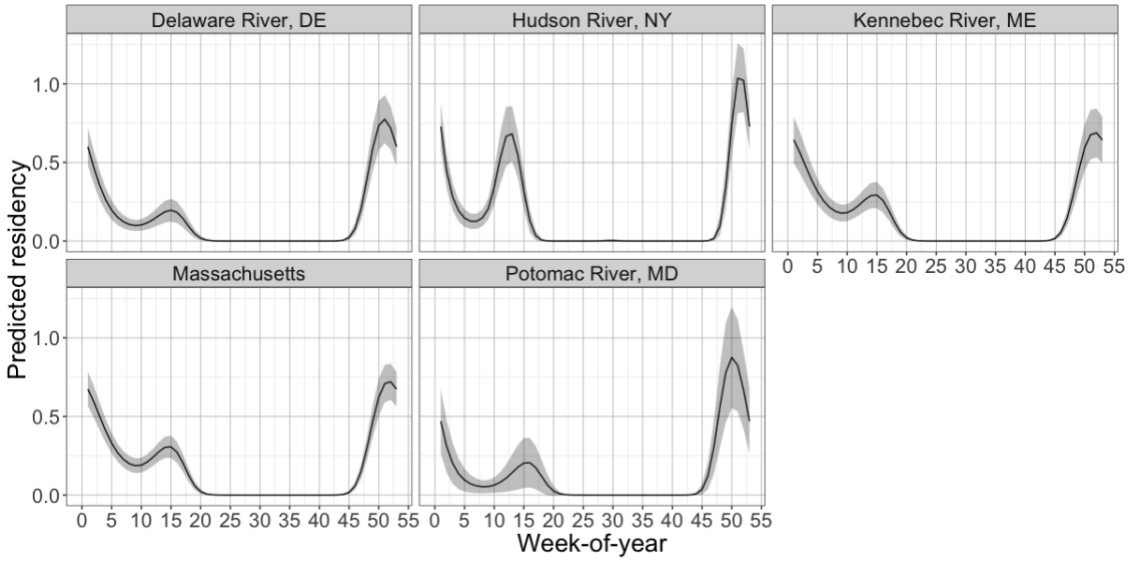

Figure 3.11. Predicted residency function (days per week ± 2 se) of striped bass in the MD WEA array for each tagging region based on week-of-year.

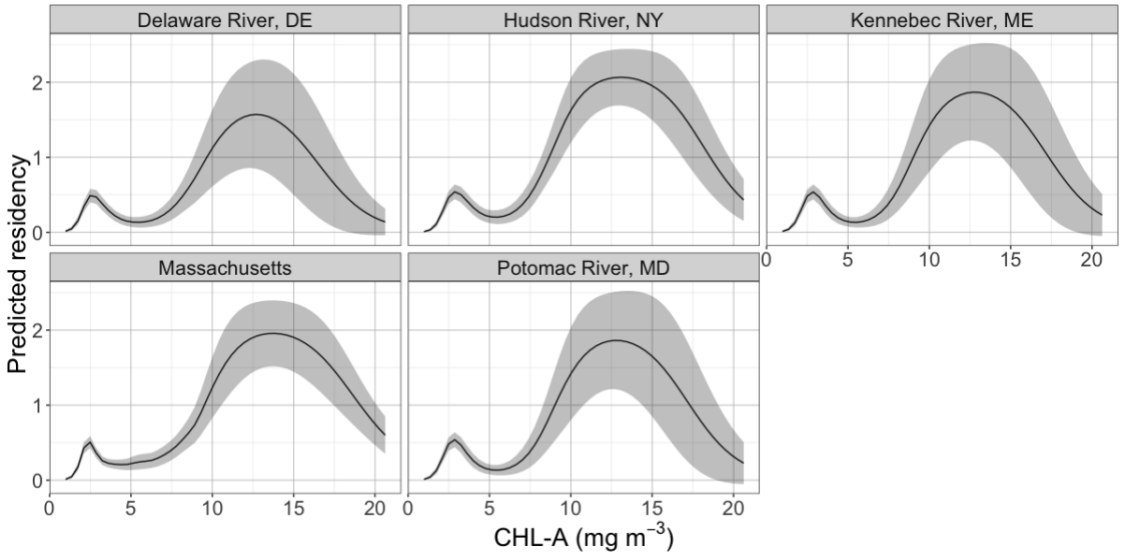

Figure 3.12. Predicted residency function (days per week ± 2 se) of Atlantic sturgeon in the MD WEA array for each tagging region based on chlorophyll-a concentration (CHL-A)

Appendices

Table A.1. Characteristics of the 40 striped bass tagged between 4/21/17 and 5/11/17 in the Lower Potomac River, Point Lookout State Park, MD and off the coast of Massachusetts. All fish were surgically implanted with depth-transponding acoustic transmitters (VEMCO®; model V16P-4H-S256; 67 mm, 10 g, 2.5 year expected battery life).

Tag Date	*Transmitter ID*	*Length (TL, cm)*	*Weight (kg)*	*Sex*	*Tagging Location*
5/11/2017	A69-9002-6757	77	5.1	Male	Potomac
9/1/2017	A69-9002-6758	81			Massachusetts
9/1/2017	A69-9002-6759	76			Massachusetts
9/1/2017	A69-9002-6760	82			Massachusetts
9/1/2017	A69-9002-6761	78			Massachusetts
9/1/2017	A69-9002-6762	86			Massachusetts
9/1/2017	A69-9002-6763	77			Massachusetts
9/1/2017	A69-9002-6764	80			Massachusetts
9/1/2017	A69-9002-6765	81			Massachusetts
9/1/2017	A69-9002-6766	114.3	19	Female	Potomac
9/1/2017	A69-9002-6767	107.3		Female	Potomac
9/1/2017	A69-9002-6768	100.3	13	Female	Potomac
9/1/2017	A69-9002-6769	100.3	13.2	Female	Potomac
9/1/2017	A69-9002-6770	107.9	17.7	Female	Potomac
9/1/2017	A69-9002-6771	106.7	16.8	Male	Potomac
9/1/2017	A69-9002-6772	97.8	13	Female	Potomac
9/1/2017	A69-9002-6773	106.7	15.6	Female	Potomac
9/1/2017	A69-9002-6774	104.1	16.8	Female	Potomac
4/21/2017	A69-9002-6775	75.7	5.1	Female	Potomac
4/21/2017	A69-9002-6776	88.6	7.2	Male	Potomac
4/21/2017	A69-9002-6777	99.8	9.8	Female	Potomac
4/21/2017	A69-9002-6778	99.8	10	Female	Potomac
4/21/2017	A69-9002-6779	99.7	11.7	Female	Potomac
4/21/2017	A69-9002-6780	89.1	8.4	Female	Potomac
5/8/2017	A69-9002-6781	81.4	6.5	Female	Potomac
5/8/2017	A69-9002-6782	80.0	5.6	Female	Potomac
5/8/2017	A69-9002-6783	98.9	10.2	Female	Potomac

5/8/2017	A69-9002-6784	87.1	6.6	Male	Potomac
5/8/2017	A69-9002-6785	81.7	9.4	Female	Potomac
5/8/2017	A69-9002-6786	101.	10.6	Female	Potomac
5/8/2017	A69-9002-6787	81.7	6.2	Male	Potomac
5/11/2017	A69-9002-6788	85.7	7	Male	Potomac
5/11/2017	A69-9002-6789	77.1	5.1	Male	Potomac
5/11/2017	A69-9002-6790	83.0	5.8	Female	Potomac
5/11/2017	A69-9002-6791	77.5	5.7	Female	Potomac
5/11/2017	A69-9002-6792	99.5	11.7	Male	Potomac
9/1/2017	A69-9002-6793	83			Massachusetts
9/1/2017	A69-9002-6794	86			Massachusetts
9/1/2017	A69-9002-6795	84			Massachusetts
9/1/2017	A69-9002-6796	75.5			Massachusetts

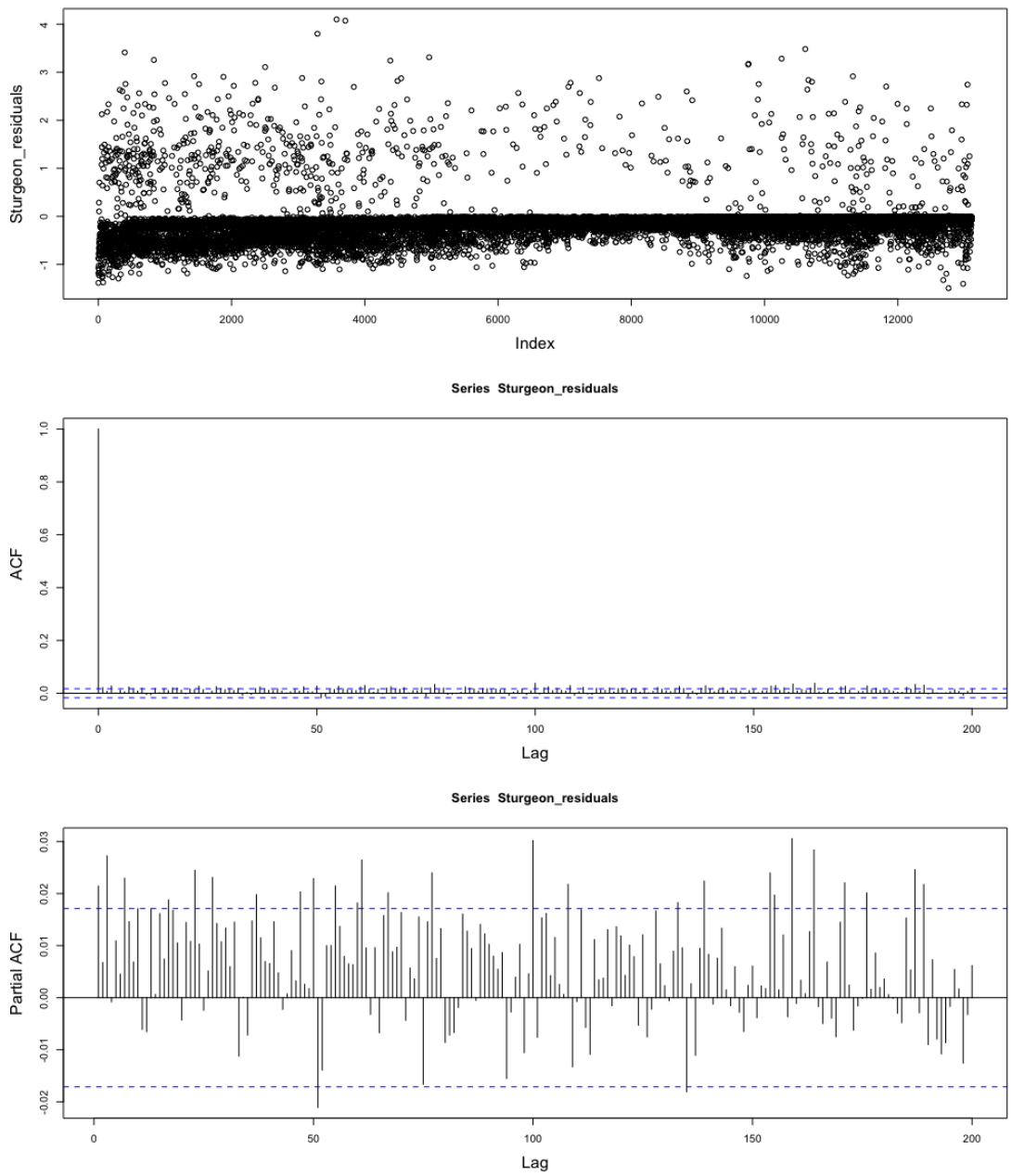

Figure A.1. Summary plots for Atlantic sturgeon relative abundance model temporal residuals showing distribution of residuals over time (top panel), autocorrelation function plot of residuals (ACF, middle panel), and partial autocorrelation plot of residuals (Partial ACF, bottom panel).

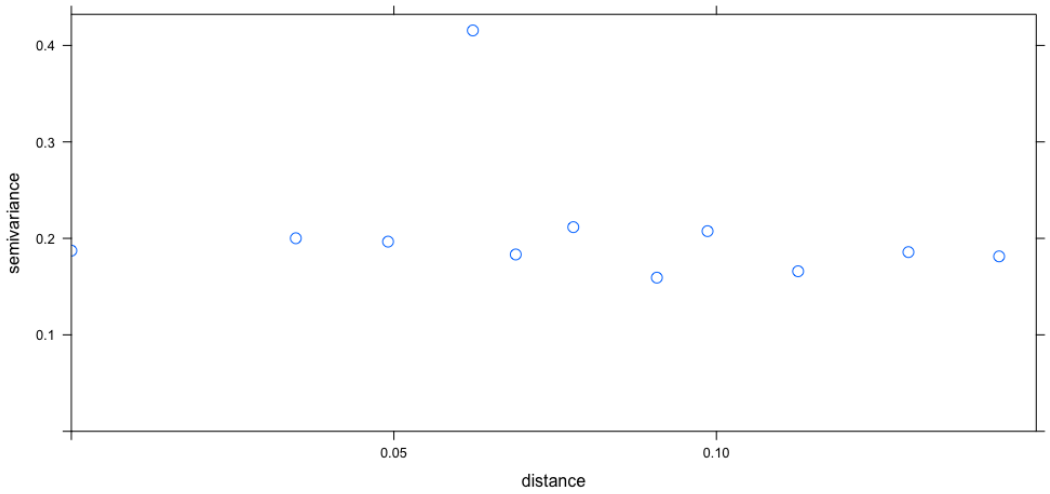

Figure A.2. Semi-variogram of residuals from best Atlantic sturgeon relative abundance model using latitude and longitude to calculate distance between sites.

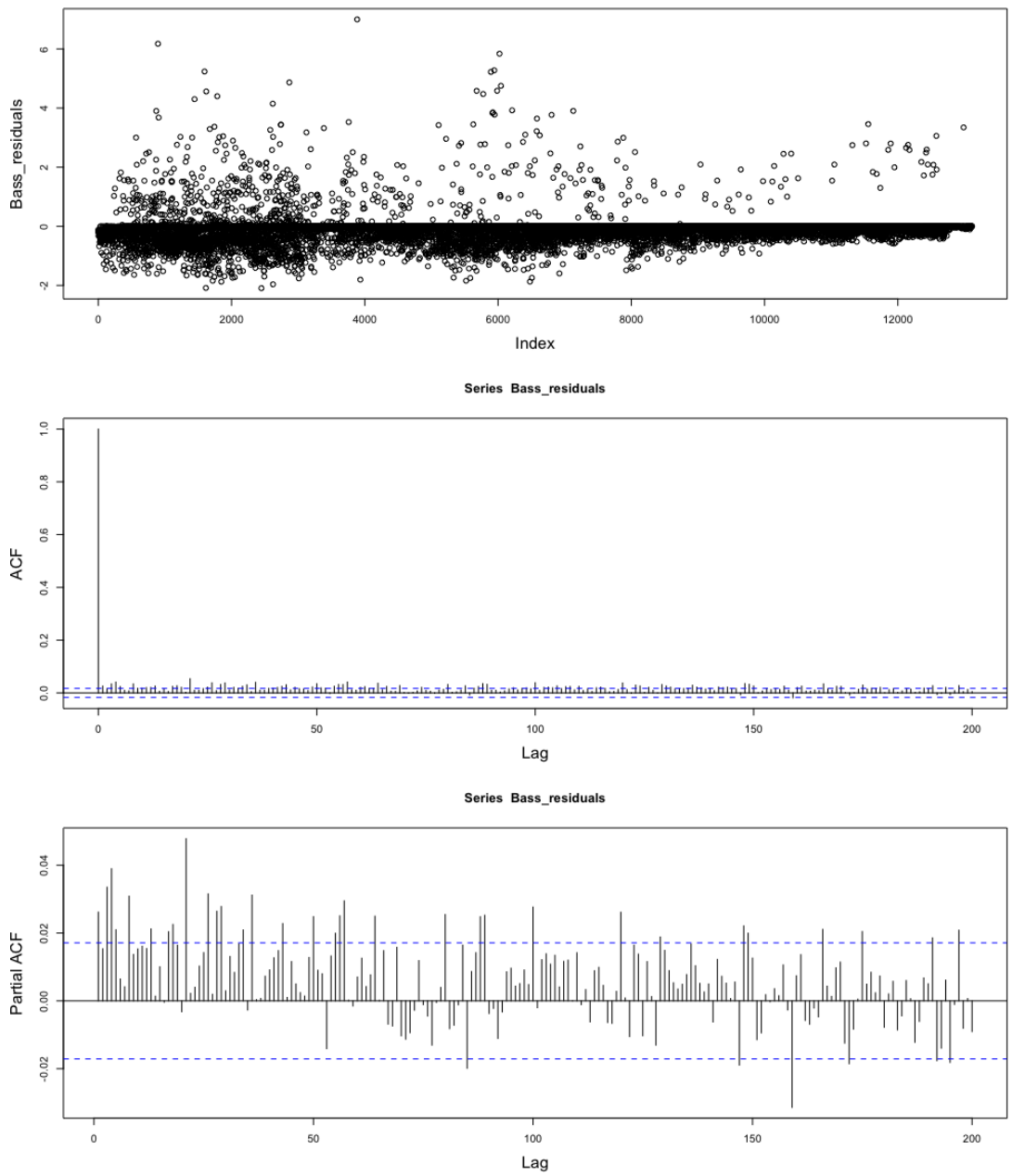

Figure A.3. Summary plots for striped bass relative abundance model temporal residuals showing distribution of residuals over time (top panel), autocorrelation function plot of residuals (ACF, middle panel), and partial autocorrelation plot of residuals (Partial ACF, bottom panel).

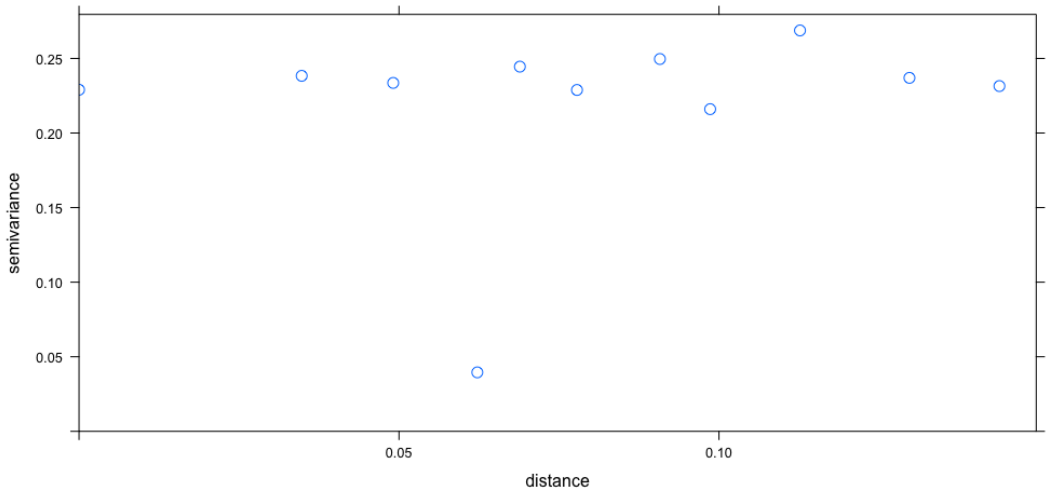

Figure A.4. Semi-variogram of residuals from best striped bass relative abundance model using latitude and longitude to calculate distance between sites.

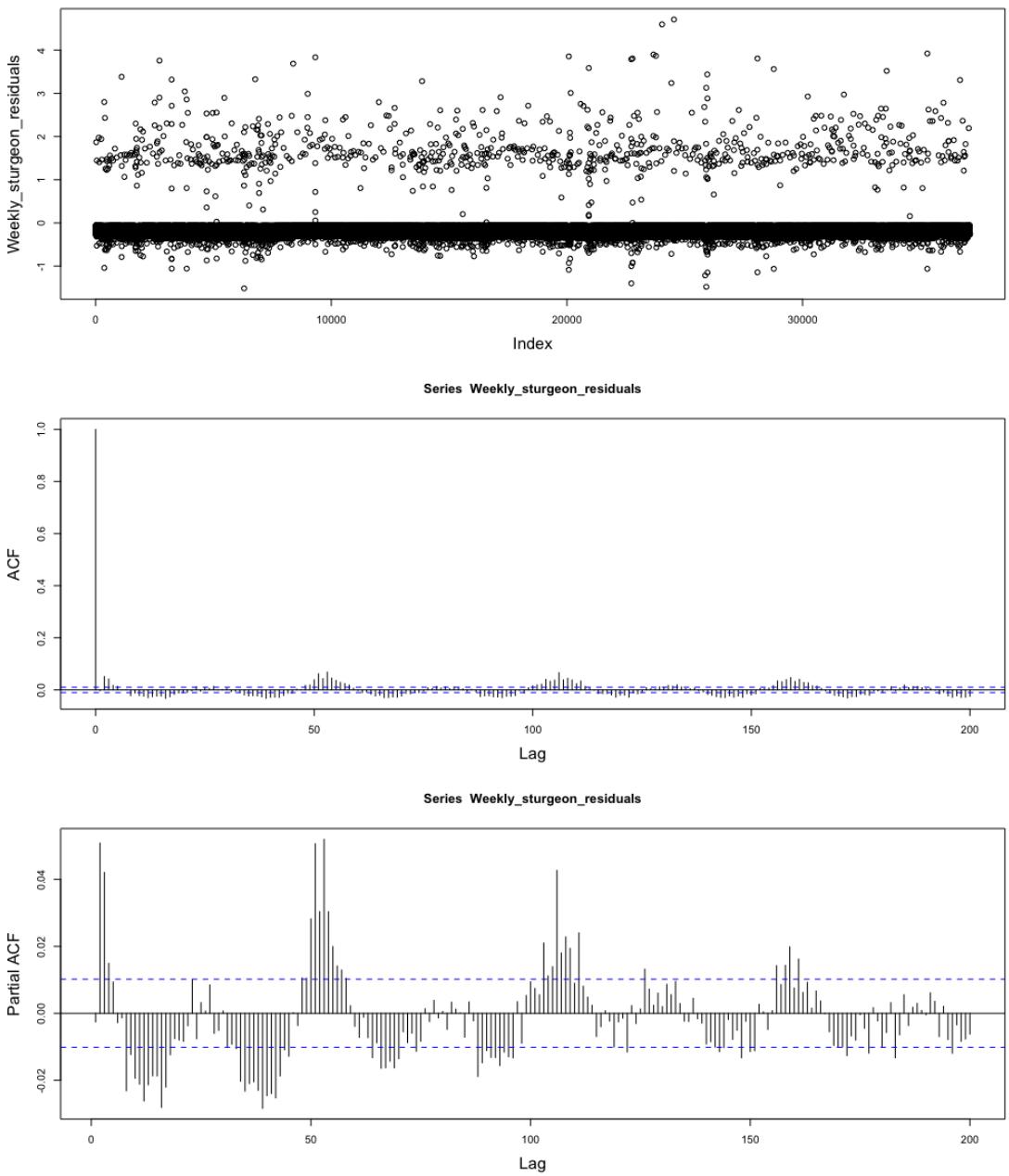

Figure A.5. Summary plots for Atlantic sturgeon weekly residency model temporal residuals showing distribution of residuals over time (top panel), autocorrelation function plot of residuals (ACF, middle panel), and partial autocorrelation plot of residuals (Partial ACF, bottom panel).

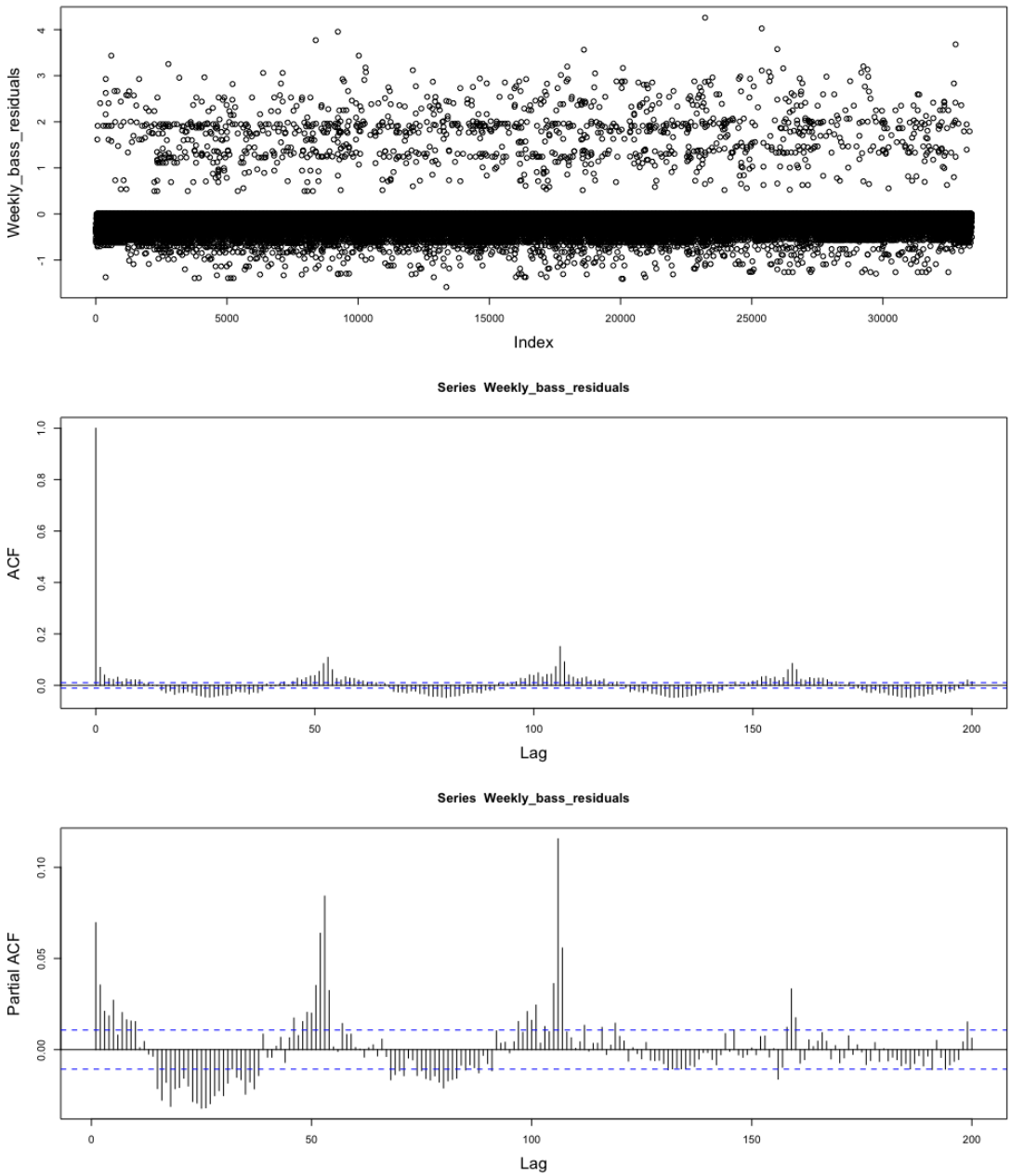

Figure A.6. Summary plots for striped bass weekly residency model temporal residuals showing distribution of residuals over time (top panel), autocorrelation function plot of residuals (ACF, middle panel), and partial autocorrelation plot of residuals (Partial ACF, bottom panel).

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